THE

PROCEEDINGS

OF THE

LINNEAN SOCIETY

OF

NEW SOUTH WALES

FOR THE YEAR

1947

VOL. LXXII.

WITH TWENTY-THREE PLATES.

219 Text-figures.

CONTENTS OF PROCEEDINGS, 1947.

PARTS I–II (Nos. 329–330).

(*Issued 23rd June, 1947.*)

PARTS III–IV (Nos. 331–332).

(Issued 15th September, 1947.)

PARTS V–VI (Nos. 333–334).

(*Issued 15th January, 1948.*)

ANNUAL GENERAL MEETING.

WEDNESDAY, 26th MARCH, 1947.

The Seventy-second Annual General Meeting was held in the Society's Rooms, Science House, Gloucester Street, Sydney, on Wednesday, 26th March, 1947.

Mr. A. R. Woodhill, B.Sc.Agr., President, occupied the Chair.

The minutes of the preceding Annual General Meeting (27th March, 1946) were read and confirmed.

PRESIDENTIAL ADDRESS.

The first complete year since the Second World War ended has come to a close and the return of many members of their normal peace-time activities has had a marked effect upon the Society. Attendance at meetings has shown a definite increase, library facilities have been more fully utilized and there has been a notable increase in the numbers of undergraduates and of more recent university graduates seeking membership.

As is usual, the first part of my address is devoted to a brief review of the Society's activities during the past year.

Parts 5–6 of Volume lxx (1945) of the PROCEEDINGS, which should have been printed on 15th December, 1945, were not issued until 15th July, 1946. Volume lxx (consisting of 345 + xli pages, thirteen plates, 215 text-figures and two maps) contained twenty-seven papers on various branches of Natural History. The volume was considerably larger than that for the preceding year, though still somewhat smaller than in pre-war days. Parts 1–2 of Volume lxxi (1946) were issued on 5th November, 1946, approximately six months late. Parts 3–4 appeared on 15th January, 1947, about four months late, and Parts 5–6 should be issued within a few weeks, so that the delay in appearance of the PROCEEDINGS, arising from industrial troubles late in 1945, is gradually being overtaken. It is of interest to note that since the cessation of hostilities there has been an increasing number of manuscripts submitted for publication as members turn from special war-time problems to their former interests.

Exchanges received from scientific societies and institutions totalled 1,229 for the year, compared with 878, 664 and 670 for the three preceding years. This very marked increase was largely due to the fact that during the year a number of foreign organizations have resumed exchange relations and forwarded back volumes of their publications covering the war years.

During the year the Council decided to establish a special book-binding fund with a view to building up an adequate reserve to meet the cost of binding journals when conditions become more normal.

In April, 1946, Messrs. S. J. Copland and J. M. Vincent were elected to fill vacancies on the Council caused by the resignation of Mr. E. C. Andrews and the death of Mr. F. H. Taylor, and in December, 1946, Professor N. A. Burges was elected to the Council to fill the vacancy caused by the resignation of Professor E. Ashby.

Since the last Annual Meeting the names of fifteen members have been added to the list, four members have been lost by death, and five have resigned.

John Honeyford Campbell, C.B.E., I.S.O., who died at Ottawa, Canada, on 29th April, 1946, was born in the North of Ireland in 1866. He came to Australia as a young man and in 1884 entered the Imperial Mint, Sydney, as a junior clerk, eventually rising to the position of Deputy Master in 1921. In August, 1925, he was appointed to take charge of the Royal Mint at Ottawa, Canada, and left Australia to take up that position in February, 1926. Mr. Campbell joined this Society in 1901 and remained a member for the remainder of his life. From the time he became a member until he left

A

Australia, he took a very active interest in the Society, serving as a Councillor from 1907 until 1926, and as Honorary Treasurer from May, 1908, until 1926. Soon after becoming Honorary Treasurer, Mr. Campbell, together with the late Mr. F. E. Grant and the father of the Society's present auditor, Mr. F. H. Rayment, effected a great improvement in the method of keeping the Society's accounts and drew up a new set of books which were substantially the same as those in use to-day.

Sir George A. Julius, who died at Killara on 28th June, 1946, was born at Norwich, England, on 29th April, 1873, the son of a Church of England clergyman who later became Primate of New Zealand. After completing his university education in New Zealand, George Alfred Julius went to Western Australia and was there employed as an engineer at Fremantle railway workshops. In 1907 he came to Sydney and founded the firm of Julius, Poole and Gibson, consulting engineers, and in 1926, when it was decided to establish the Council for Scientific and Industrial Research, he was appointed Chairman, a position which he held until his retirement in 1945. By the general public he will be remembered as the inventor of the ingenious automatic totalisator which has now been installed in many countries. Sir George Julius played an important part in the foundation and development of The Institution of Engineers, Australia, and the Standards Association of Australia, and he took an active interest in the Australian National Research Council. He joined this Society in 1930.

Carl Adolph Sussmilch, who died on 6th December, 1946, was born at Sydney on 12th February, 1875. He was educated at Fort Street High School and Sydney Technical College. Later he attended Sydney University and gained Honour passes in geology, mining and metallurgy. In 1899 he joined the New South Wales Department of Education and was appointed Lecturer-in-charge of the Department of Geology and Mining, Sydney Technical College, in 1903. From 1914 until 1927 he was Principal of the Newcastle Technical College, and during 1923–24 he visited many technical schools and universities in Europe. In 1927 he became Principal of the East Sydney Technical School and Assistant Superintendent of Technical Education, and from 1934 until his retirement in 1936 he was Acting Superintendent of Technical Education. Mr. Sussmilch served on the Council of the Royal Society for many years, being President in 1922. He was awarded the Clarke Memorial Medal by the Royal Society of New South Wales in 1939 and delivered the Clarke Memorial Lecture in 1941. He joined this Society in 1904 and served on the Council for a period of twelve years between 1933 and 1946 and was President in 1936–37. Mr. Sussmilch represented the Royal Society of New South Wales at the first meeting of the Management Committee of Science House, held on 27th December, 1928. He took a very active part in the planning of the building, and after the completion of Science House until a few months before his death, except for short periods, he was a member of the Management Committee, either as a representative of the Royal Society of New South Wales or of this Society. He was a Trustee of the Australian Museum for several years and for some years until shortly before his death he was a member of the Board of Directors of the New South Wales Society for Crippled Children. Mr. Sussmilch published his book, "An Introduction to the Geology of New South Wales", in 1911, and he also published a number of geological papers in the *Journal of the Royal Society of New South Wales* and in these PROCEEDINGS. He was a Fellow of the Geological Society of London and also of the American Geological Society.

Mr. Ralph Ellis, of the University of Kansas, U.S.A., life member, who joined the Society in 1932, died during the year.

Following the visit of the survey party to the Kosciusko State Park early in 1946, a detailed report was prepared and submitted to the Kosciusko State Park Trust. The report set out the results achieved and made recommendations concerning the setting aside of natural history reserves, and other matters connected with the preservation of the native flora and fauna in the Park. During the year members of the survey party delivered a number of lecturettes on the geology, geography, zoology and botany of the Park at Ordinary Meetings of the Society.

The nett return from Science House exceeded that received in any previous year and the building is proving to be a valuable asset to the Society. When feasible, the

Management Committee proposes to improve the lighting and install modern projection equipment in the Large Hall. During the year the question of the desirability and feasibility of establishing a combined library and reading room in the proposed extension of Science House was discussed by representatives of the three owner-bodies, but as yet no final decision has been made.

We offer congratulations to Mr. E. C. Andrews on the award of the Mueller Memorial Medal by the Australian and New Zealand Association for the Advancement of Science; to Dr. W. L. Waterhouse on his appointment to a Research Professorship in the School of Agriculture, University of Sydney; to Dr. N. A. Burges on his appointment to the Chair of Botany in the University of Sydney; to Dr. S. Warren Carey on his appointment to the Chair of Geology in the University of Tasmania; to Mr. F. V. Mercer on the award of a Sydney University Commonwealth Research Fellowship, and to Mr. F. L. Milthorpe on the award of the Farrer Research Scholarship.

The year's work of the Society's research staff may be summarized thus:

Dr. H. L. Jensen, Macleay Bacteriologist to the Society, together with Mr. D. Spencer, B.Sc. (at that time an Honours student in biochemistry), has conducted an investigation of the effect of molybdenum on nitrogen fixation by *Clostridium butyricum* and related anaerobic organisms. Molybdenum was found to be essential for nitrogen fixation, but not for growth with combined nitrogen, and to be replaceable only by vanadium, and this in some strains only. Both metals represent typical "trace elements", active in concentrations as low as 0.4–0.5×10^{-8} molar. The results favour the hypothesis that the mechanism of biological nitrogen fixation is essentially the same in all nitrogen-fixing organisms. Additional observations suggest that calcium is not essential for nitrogen fixation by *Cl. butyricum* or perhaps even by leguminous plants.

The experiments on the influence of hydrogen ion concentration on symbiotic nitrogen fixation in lucerne and subterranean clover have been concluded. The inhibitory effect of acid soil reaction (pH 4.7–5.0) has been found to be much more pronounced under conditions of partial molybdenum deficiency than when an adequate supply of this element is provided. A molybdenum content of some 4 to 8 parts per million of dry root-nodule substance appears necessary for full nitrogen-fixing efficiency of the nodule-tissue. A paper dealing with these experiments is in course of preparation.

Miss Frances M. V. Hackney, Linnean Macleay Fellow of the Society in Plant Physiology, carried out further investigations on the respiratory metabolism of sliced apple tissue supplied with various respiratory substrates and inhibitors. The results obtained during 1946 confirmed those obtained with apples of similar maturity during 1945. An enzyme preparation having the properties of ascorbic acid oxidase was obtained from several varieties of apple. Its properties were studied in detail. The response of cut apple tissue to added ascorbic acid indicated that ascorbic acid oxidase might be concerned in the respiratory metabolism. The enzyme polyphenolase was prepared from Granny Smith apples and its properties were studied in detail. The results indicated that this enzyme is probably very important in the respiratory metabolism of the apple.

Miss June Lascelles, Linnean Macleay Fellow of the Society in Biochemistry, continued her studies on the oxidation of molecular hydrogen by *Escherichia coli*. Using washed cells of *E. coli*, the properties of the system responsible for the uptake of molecular hydrogen in the presence of fumarate have been studied in detail. As would be expected, analysis revealed that succinate accounted for most of the disappearing fumarate. However, there was a large reduction of fumarate by donators within the washed cells, so that hydrogen uptake did not account for the total amount of fumarate disappearing. Interference by these substrates within the cells was eliminated by treatment of the suspensions with toluene under certain conditions. Such treatment also appeared to increase markedly the rate of hydrogen uptake in the presence of fumarate; this was thought to be caused by the increased permeability of the bacterial cells to fumarate, after treatment with toluene. It was shown that the hydrogen-fumarate system of *E. coli* is dependent upon certain diffusible factors, which have yet to be determined. Studies with inhibitors were carried out, using normal and toluene-treated cells. Some marked differences were noted with these two types of enzyme preparation, in their reactions to certain inhibitors, notably the nitrophenols. The

uptake of molecular hydrogen in the presence of malate was studied also. It would appear that the enzyme, fumarase, converts the malate to fumarate, before uptake of molecular hydrogen occurs. The hydrogen-malate system was inactivated by toluene treatment under those conditions which resulted in an increase in the activity of the hydrogen-fumarate system. Otherwise, the properties of the two systems were mainly identical. The results of these investigations have been recorded in a paper which will shortly be published in these PROCEEDINGS. Also, investigations were begun on the oxidation of molecular hydrogen in extracts of *E. coli* obtained by crushing the cells with ground glass. The systems responsible-for the uptake of hydrogen in the presence of methylene blue, nitrate, fumarate, malate and molecular oxygen were present in these extracts.

Only one application for a Linnean Macleay Fellowship was received in response to the Council's invitation of 25th September, 1946, and I have pleasure in reminding you that the Council reappointed Miss June Lascelles, M.Sc., to a Fellowship in Biochemistry for one year from 1st March, 1947. The decline in the number of applications for Fellowships in recent years is undoubtedly due to the declining real value of money. The result is that, today, the Fellowships, which were once most attractive to first-class research workers, compare unfavourably with other Fellowships which are now available. The Council has already given some consideration to this problem.

During the coming year Miss Lascelles proposes to investigate the systems connected with hydrogenase in extracts of *E. coli*, and an attempt will be made to identify and classify them. She will also investigate the properties of the enzyme, formic hydrogenlyase, present in the cells of *E. coli*. We wish her success in her coming year's work.

A BRIEF REVIEW OF PROGRESS IN THE CONTROL OF SOME MAJOR AGRICULTURAL INSECT PESTS
IN NEW SOUTH WALES DURING THE PERIOD 1920–1945.

INTRODUCTION.

The period under review is one of considerable interest in relation to the development of applied entomology in New South Wales, and indeed, throughout Australia, since the early nineteen-twenties were marked by a very great expansion in entomological research, the effects of which became obvious during th following twenty years. Prior to 1920 the number of research workers was extremely limited. The Entomological Branch of the New South Wales Department of Agriculture had, at that time, a staff of three only, and the Division of Economic Entomology of the Council for Scientific and Industrial Research had not been formed. By 1930, however, the staff of the Entomological Branch had increased to eight, and that of the Division of Economic Entomology numbered sixteen, all the members of these institutions being actively engaged on various problems in applied entomology. This change was brought about by the more enlightened policy adopted by State and Federal Governments, and in particular by the establishment of scientific cadetships and the formation of the Council for Scientific and Industrial Research. In addition, the establishment, in 1922, of a full-time lectureship in Economic Entomology in the University of Sydney, provided a means whereby research workers in entomology could be trained.

During the period under consideration a great number of carefully controlled field experiments on the direct control of insect pests was carried out by the New South Wales Department of Agriculture, and towards the latter part of the period, the principles of statistical analysis were increasingly applied to this work. The Division of Economic Entomology of the Council for Scientific and Industrial Research also carried out numerous field experiments in direct control, but in addition, gave increasing attention to fundamental studies on the ecology, physiology, population density and natural controlling factors associated with insects, and as a result, a much clearer understanding of many of our insect pest problems was attained. Biological control of insect and plant pests was also undertaken both by the New South Wales Department of Agriculture and the Council for Scientific and Industrial Research, and in recent years, much more attention has been paid by the latter institution to the subject of insect toxicology.

FRUIT-FLIES.

(*Strumeta tryoni* and *Ceratitis capitata.*)

Fruit-flies are probably the most serious pests of stone and pome fruits in coastal areas. At the beginning of the period under review, control measures consisted in trapping and the destruction of infested fruit, and whilst these gave some measure of control, it was by no means satisfactory. During the early 1920's, a method known as the foliage bait spray was evolved; this consisted in spraying small patches of foliage with a mixture of some sweet syrup and an arsenical, which would both attract and poison the flies. This proved much-more efficient and economical than trapping, and later the bait spray was greatly improved as the result of experiments with various insecticides and syrups, the most efficient being a mixture of sugar solution with sodium fluosilicate or tartar emetic. Recently, frequent sprayings with a mixture of sugar solution and nicotine sulphate have given very promising results. Whilst fruit-fly control in home gardens in densely populated areas is extremely difficult owing to the continuous influx of flies from untreated adjacent trees, there is no doubt that adequate control can now be obtained on a commercial scale where large areas of trees are treated, and the position has changed greatly since 1920.

THE GREEN PEACH APHID.

(*Myzus persicae.*)

This is one of the most serious pests of peaches, particularly in the Murrumbidgee Irrigation Area. When uncontrolled, enormous numbers of aphids develop on the young growth in spring and early summer, almost completely destroying the foliage and causing heavy losses of crop. In the early 1920's control was quite inadequate, red oil being recommended as a dormant spray for the overwintering eggs, and nicotine sulphate as a spring and summer spray; but the oil was inefficient as an ovicide and the curled leaves later in the season gave sufficient shelter to the aphids to prevent adequate control by nicotine sprays. At this time the details of the seasonal appearance of the various forms of the aphid were not known, and consequently, the most vulnerable points in the life cycle were not attacked. As a result of bionomical studies it was shown that all the overwintering eggs were deposited by the middle of June and remained unhatched until the middle of July; there was then a brief period from 5th to 25th August during which all the eggs had hatched to wingless adult aphids, but the peach buds had not yet burst. About this time a type of tar distillate spray had been developed in England, and this gave 100% kill of aphid eggs, but could only be used on dormant trees. It was recommended, therefore, that tar distillate sprays be applied from mid-June to mid-July (while the trees were dormant) and nicotine sprays between 5th and 25th August when the recently-hatched aphids were completely exposed and could not gain access to the closed buds. Either of these sprays, if applied correctly at the right time, now gives almost complete control, as compared with total inability to control the pest in 1920. The method is an excellent example of accurate correlation of time of spraying with particular stages in the development of a pest and its host plant. Sprays composed of di-nitro-cresol, in the latter part of the period, replaced the original tar distillate sprays and had the advantage of being less objectionable for the operators and less severe on the trees.

THE CODLING MOTH.

(*Cydia pomonella.*)

This is, of course, a major pest of pome fruits throughout the world, and if uncontrolled can result in almost a complete loss of crop. The standard methods of control, which were in use in 1920 and which are still practised, consist of applying a series of arsenate of lead sprays during the growing period of the fruit, destroying overwintering larvae by the use of trunk bandages, and the destruction of infested fruit. At the beginning of the period, these methods were giving reasonable control, but nevertheless severe losses often occurred. Considerable research was directed towards working out the detailed bionomics of the pest under local conditions and to improving the efficiency

and timing of the arsenate of lead sprays. By the proper use of sprays, and strict attention to larval destruction and orchard sanitation throughout the year, it was found to be possible to reduce the infestation of the crop from 80% to 4%. One important factor in obtaining this result was the incorporation of a small percentage of miscible white oil with some of the arsenate of lead sprays. Nevertheless, control of this extent is not always attained even under the strictest supervision, and since adequate control necessitates the application of six separate sprays, it is obvious that any new method which would reduce the cost of control is very desirable. It will be clear from the above that considerable advances have been made during the period under review, but that further improvement is desirable, and work in this direction is proceeding.

THE WOOLLY APHID.
(*Eriosoma lanigerum.*)

This again is a major pest of pome fruits, and at the beginning of the period, it was practically impossible to control it even with six or eight sprayings of nicotine sulphate during the spring and summer, owing to the fact that the aphids also occur on the roots, and when above ground are particularly well protected. During the early 1920's, however, a parasitic Chalcidoid wasp, *Aphelinus mali*, was introduced and rapidly became established in all the main apple growing centres. It is now present wherever apples are grown in New South Wales, and has effected complete commercial control of the pest. This is, in fact, the most outstanding success in the field of biological control of insect pests in Australia.

THE BLACK PEACH APHID.
(*Anuraphis persicae-niger.*)

This is one of the most difficult pests to control as the aphids occur on the roots as well as the above-ground portion of the tree and the only control has consisted of repeated sprayings with nicotine sulphate. Practically no improvement had been made in control methods up to 1944, but there are indications that remarkably efficient control will be obtained in the future by the use of D.D.T.

THE DICKY RICE WEEVIL.
(*Maleuterpes phytolymus.*)

This is a small weevil which breeds on the roots of citrus trees, but, unlike the Fruit Tree Root Borer, it does not damage the roots sufficiently to cause marked injury to the trees. The loss is incurred as a result of the adult beetles feeding on the skin of the young fruit, which, when it matures, is disfigured by black irregular markings, and thus the market value of the crop is considerably lowered. At the beginning of the period, no control was available, but experiments rapidly demonstrated that adequate banding with tree-tanglefoot, at the correct time of the year, would reduce the percentage of marked fruit to a negligible figure.

THE RED MITE.
(*Bryobia praetiosa.*)

This mite, which is a pest of both pome and stone fruits, is capable of causing considerable injury, but it can be satisfactorily controlled by properly timed sprays consisting of various sulphur compounds. Control methods were satisfactory at the beginning of the period under review and remain so at the present time.

THE FRENCH BEAN FLY.
(*Agromyza phaseoli.*)

This insect is extremely common wherever beans are grown on the coast of New South Wales, north of Sydney, and it is particularly abundant from December to April, so that in many districts, at the beginning of the period under review, it was almost impossible to grow summer and autumn crops of beans, since no satisfactory method of control was available. The damage is caused by the larvae, which feed under the

skin of the main stem of the young plants, completely destroying them. Detailed bionomical studies eventually revealed that the eggs were laid in the leaves and that the larvae at first behaved as leaf miners before making their way to the stem. It was found that in the leaf-mining stage they could be reached by a contact spray, and a carefully timed series of sprays composed of nicotine and white oil emulsion gave highly satisfactory control. It is not too much to say that as a result of entomological research it is now possible to grow profitable crops of beans throughout the summer and autumn, and that the problem of the control of the French Bean Fly has been successfully solved.

CUTWORMS.
(Family Noctuidae.)

A number of species of cutworms are important pests of many kinds of vegetable crops and occur in plague proportions from time to time, causing extremely heavy losses. The larvae harbour in the soil during the day-time and emerge at night to feed on plant stems or foliage. At the beginning of the period, satisfactory control was obtained by the use of poisoned bran baits and this is still the standard method. Considerable research has been carried out on the biology of these insects with the result that the general technique of control has been considerably improved, but no revolutionary change has taken place.

THE BROWN VEGETABLE WEEVIL.
(Listroderes obliquus.)

This is an introduced pest which was first recorded about 1905 and continued to become more and more abundant until by 1920 it was one of the most injurious pests of vegetables. At this time little was known of its biology and no control methods had been worked out. By 1924, however, intensive research had been carried out on its life history and habits, and completely satisfactory control was obtained by spraying and baiting with arsenicals combined with the destruction of its alternative host plants.

THE CABBAGE MOTH.
(Plutella maculipennis.)

This is a very widespread and destructive pest of cabbages and cauliflowers, and if uncontrolled, usually causes complete loss of the crop. Prior to 1920, the control of this pest was quite unsatisfactory but by the early 1930's a highly successful schedule of dusting with arsenate of lead and derris had been worked out, and this, combined with the improvement in dusting machinery and technique, now enables the grower to obtain something over 90% control with comparative ease and certainty.

THE GREEN VEGETABLE BUG.
(Nezara viridula.)

This insect has a very wide range of host plants, but is particularly injurious to beans and tomatoes. The adult bugs are extremely resistant to most of the commonly used insecticides, and at the beginning of the period under review, control by direct means was virtually impossible. Later, research showed that the early stages could be controlled to some extent by spraying with derris and soap solutions, but the position remained highly unsatisfactory until the introduction of the parasite Microphanurus basalis in 1930. This is a minute Chalcidoid wasp which is a parasite of the eggs of Nezara viridula, and which was originally introduced from Egypt to Western Australia and from there to New South Wales. Supplies of the parasite have been bred up and distributed over a number of years throughout the State (approximately 50,000 parasites were distributed in New South Wales in 1944), and it is now definitely established in all areas where the bug occurs. In coastal regions of New South Wales the control obtained by the introduction of this parasite is highly satisfactory, though in inland areas its effect at present is not so marked.

THE POTATO MOTH.

(*Gnorimoschema operculella.*)

At the beginning of the period, control was limited to the fumigation of infested potatoes in storage. This was by no means satisfactory as only partial control could be obtained and frequently considerable loss occurred before the potatoes were harvested. Later, research showed that the early development of the larvae took place in the leaves and stems of the growing plant, while the tubers were infested in the field before harvesting. Recent research work has been directed towards controlling the early stages in the green portion of the plant and preventing infestation of tubers, and it has been shown that regular applications of derris dusts or sprays, combined with "hilling" at the correct time, will give very satisfactory control.

THE BLACK BEETLE.

(*Heteronychus sanctae-helenae.*)

This is an introduced pest which was first recorded in this country some twenty years ago and has become increasingly abundant and destructive in coastal areas in New South Wales. It is a particularly serious pest of early sown maize, sugar-cane sets and many vegetables. When it first appeared, nothing was known of the life cycle, but later, research showed that the beetles overwintered in the adult stage and became active during September and October. By the end of October, the majority of the beetles have deposited their eggs and died, and these eggs develop to adult beetles by January and February. There are thus two periods when the adults are abundant and active, but most of the damage is caused by the overwintering beetles as they become active in September and commence to attack early maize and vegetables. Research has shown that losses may be largely prevented by timing the sowing of crops to avoid the peak period of abundance of the beetles. In addition, the dipping of cane sets in an adhesive arsenical mixture has been shown to be quite effective. By these means some control has been obtained, but more satisfactory methods are still necessary, and gammexane and D.D.T. are showing great promise.

THE MAIZE AND TOMATO CATERPILLAR.

(*Heliothis obsoleta.*)

This is a cosmopolitan pest known in America as the Corn Ear Worm; in Australia its chief importance is as a pest of tomatoes, although many other plants are also attacked, the caterpillars feeding mainly in the reproductive portion of the plant. Arsenical sprays and dusts are widely used for the control of this insect, and, in New South Wales, research has been largely directed towards working out a suitable spray schedule for protecting tomatoes. While the control is still not entirely satisfactory, considerable improvement has been brought about during the period under review.

THE RED SPIDER.

(*Tetranychus urticae.*)

This is an introduced mite which infests various weeds, field crops, shrubs and trees, but is a particularly serious pest of beans and peas. At the beginning of the period under review, it was known that various sulphur preparations gave adequate control, and later research has largely been directed towards improving the effectiveness of sulphur dusts and sprays, so that at the present time control of red spider does not present any serious difficulties.

THE AUSTRALIAN PLAGUE LOCUST.

(*Chortoicetes terminifera.*)

This pest occurs mainly in the central division of New South Wales and is always present to some extent, but from time to time it reaches plague proportions, in what are known as "grasshopper years", and causes enormous losses in pastures and crops, the flying swarms spreading over a great area and completely destroying any crops or herbage on which they alight. In the early part of the period, sodium arsenite sprays

were used, but later work showed that poisoned bran baits were far more effective and economical, and much less dangerous to stock. The success or failure of plague locust control depends entirely on the concerted efforts of the land-holders and on the degree of co-operation which is developed, since individual efforts have only a negligible effect. Considerable progress has been made in this co-operative effort by organization of the Pastures Protection Boards, and by supplying these bodies with mixing machines which facilitate the preparation of the bait. Effective plague locust control is difficult but nevertheless considerable progress has been made, although a more concerted effort on the part of land-holders and Pastures Protection Boards is needed. A great amount of fundamental research work on the biology and ecology of this pest has been carried out, and we now have a much sounder knowledge of the factors responsible for outbreaks. This in turn may lead to some ecological method of control being eventually developed.

SHEEP BLOWFLIES.
(*Lucilia* spp., *Chrysomyia* spp. and *Calliphora* spp.)

Sheep blowflies constitute the major pest of Australia's principal primary industry and it is therefore not surprising that a very great amount of research work on this problem has been carried out by entomologists, chemists and veterinarians in the last twenty-five years. At the commencement of the period under review, emphasis was laid on the necessity for reducing the fly population by poisoning of carcases, trapping of adult flies and the use of parasites, but as a result of intense and prolonged research work on the biological aspects of the problem, it has been clearly demonstrated that under Australian conditions economical control can only be obtained by prevention of fly strike, i.e., control on the sheep, rather than by control of the fly population. In addition, the knowledge gained of the fundamental biological principles involved in the blowfly problem has undoubtedly prevented much wasteful expenditure on control experiments carried out on unsound lines. In 1920 the only control consisted of cleaning and dressing struck sheep, which was a very expensive and time-consuming method, rendering effective control almost impossible in a bad fly period, particularly since many of the dressings used at this time were unsatisfactory. Some rather haphazard work had been carried out previously in jetting with sodium arsenite, but it was not until 1930 that systematic jetting experiments were commenced, and these eventually demonstrated that four to six weeks' protection from fly strike could be obtained by the use of calcium arsenite. At the same time it was shown that merino sheep could be classified into three main groups according to their susceptibility to fly strike, these differences being correlated with the degree of wrinkling of the breech. The breeding of plain-bodied non-susceptible merinos was therefore advocated, but as this is a lengthy process, experiments were carried out to determine whether the same results could be obtained by surgical removal of the breech wrinkles, i.e., "Mule's operation". This operation, if properly carried out, has been shown to give most spectacular results, in many cases reducing fly strike in bad fly periods by as much as 90%, without any significant mortality among the sheep as a result of the operation. It can be stated, therefore, that by a judicious combination of crutching, jetting and the Mule's operation, it is now possible economically and effectively to prevent fly strike in sheep. In addition, the dressings used for remedial treatment have been greatly improved and can now be considered quite satisfactory.

SUMMARY.

From the foregoing review it will be seen that, on the basis of improved methods of control developed in the intervening twenty-five years, the twenty pests listed may be grouped as follows:

(a). *1920—Control either not possible or very poor.*
1945—Control highly satisfactory.
       Fruit Tree Weevil.*
       Fruit-Flies.
       Green Peach Aphid.

* For citrus only, not satisfactory for pome and stone fruits.

Woolly Aphid.
Dicky Rice Weevil.
French Bean Fly.
Brown Vegetable Weevil.
Cabbage Moth.
Green Vegetable Bug.
Potato Moth.
Sheep Blowflies.

(b). *1920—Control fairly satisfactory.*
1945—Control considerably improved.
Red Scale.
Codling Moth.
Cutworms.
Maize and Tomato Caterpillar.
Australian Plague Locust.
Red Spider.

(c). *1920—Control satisfactory.*
1945—Control satisfactory.
Red Mite.

(d). *1920—Control unsatisfactory.*
1945—Control slightly improved.
Black Peach Aphid.
Black Beetle.

The fact that eleven out of thirteen pests which were practically uncontrollable in 1920 can now be satisfactorily controlled, and that the control of six others has been considerably improved, indicates the practical value to the agriculturalist of entomological research carried out during the past 25 years, and justifies increased expenditure in the future. However, control classed as highly satisfactory can not be regarded as perfect; the only perfect method is one by which permanent control is established without annual recurrent expenditure, i.e., by means of parasites or predators, alteration of farm practice, or the use of resistant varieties. Any direct insecticidal method of control entails annual expenditure, and any improvements which will reduce the cost or increase the efficiency will directly lower the cost of production and increase the growers' profits.

Numerous common pests have, of course, been omitted from this review, but the general position indicated in this selection can be taken to apply also to the remainder.

The outlook for the future is extremely hopeful in view of the potent nature of various new insecticides now coming into use, and it is probable that the next twenty-five years will be marked by even more rapid advances in the control of insect pests.

Acknowledgements.

The author is greatly indebted to Mr. T. McCarthy, Chief Entomologist, New South Wales Department of Agriculture, for helpful information and criticism in the compilation of this review, and to Mr. R. N. McCulloch for advice on the section dealing with sheep blowflies.

————————

The Honorary Treasurer, Dr. A. B. Walkom, presented the Balance Sheets for the year ended 28th February, 1947, duly signed by the Auditor, Mr. S. J. Rayment, F.C.A. (Aust.); and he moved that they be received and adopted, which was carried unanimously.

No nominations of other candidates having been received, the Chairman declared the following elections for the ensuing year to be duly made:

President: G. D. Osborne, D.Sc., Ph.D.

Members of Council: R. H. Anderson, B.Sc.Agr., W. R. Browne, D.Sc., Professor N. A. Burges, M.Sc., Ph.D., A. N. Colefax, B.Sc., S. J. Copland, B.Sc., J. M. Vincent, B.Sc.Agr.

Auditor: S. J. Rayment, F.C.A. (Aust.).

A cordial vote of thanks to the retiring President was carried by acclamation.

GENERAL ACCOUNT. Balance Sheet at 28th February, 1947.

LIABILITIES.

	£ s. d.	£ s. d.	£ s. d.
Capital—			
Amount received from Sir William Macleay during his lifetime ..	14,000 0 0		
Further sum bequeathed by his Will	6,000 0 0		
		20,000 0 0	
Contingencies Reserve		9,231 18 1	
Accumulated Funds			29,231 18 1
Suspense	15 0 0		
Bookbinding Account	104 12 3		
Current Liabilities			119 12 3
			£29,351 10 4

ASSETS.

	£ s. d.	£ s. d.	£ s. d.
Fixed Assets—			
Commonwealth Loans, at cost		3,000 0 0	
Debentures:			
Metropolitan Water, Sewerage and Drainage Board, at cost ..		494 7 6	
Society's Freehold, at cost		11,000 0 0	
Science House (one-third share), at cost		14,715 0 0	
			29,209 7 6
Current Assets—			
Commercial Banking Company of Sydney Ltd.	45 2 4		
Income Account	87 0 6		
Cash in hand	10 0 0		
			142 2 10
			£29,351 10 4

INCOME ACCOUNT. Year Ended 28th February, 1947.

	£ s. d.	£ s. d.
To Balance from 1945-46		78 5 0
" Salaries		960 0 0
" Printing Publications	601 1 6	
" Illustrations	114 15 3	
		715 16 9
" Rates and Insurance		243 4 2
" Postage	52 13 0	
" Petty Cash	27 15 7	
		80 8 7
" Audit	10 10 0	
" Printing, etc.	32 6 0	
" Expenses	47 17 3	
" Attendance and Cleaning	26 0 0	
" Library	12 11 0	
" Bank Expenses	1 3 0	
		130 7 3
" Transfer to Bookbinding Account ..		104 12 3
		£2,312 14 7

	£ s. d.	£ s. d.
By Subscriptions: 1946-47	154 7 0	
Arrears	16 16 0	
In advance ..	10 10 0	
		181 13 0
" Entrance Fees		16 16 0
" Rent		472 11 4
" Interest		345 12 6
" Science House		632 0 0
" Sales (including 60 copies of PROCEEDINGS purchased by Government of N.S.W.) ..		264 12 3
" Fellowships Account (surplus income at 28th February, 1947, transferred)		312 9 0
" Balance to 1947-48		87 0 6
		£2,312 14 7

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1947, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1947, as shown by the books. Certificates of the investments have been inspected.

S. J. RAYMENT, Chartered Accountant (Aust.), Auditor.

Sydney, 12th March, 1947.

A. B. WALKOM, Hon. Treasurer

4th March, 1947.

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

BALANCE SHEET at 28th February, 1947.

LIABILITIES.

	£	s.	d.
Accumulated Funds—			
Amount bequeathed by Sir William Macleay	35,000	0	0
Surplus Income Capitalized	15,713	18	11
	£50,713	**18**	**11**

ASSETS.

	£	s.	d.	£	s.	d.
Fixed Assets—						
Commonwealth Loans, at cost	29,850	0	0			
Debentures:						
Metropolitan Water, Sewerage and Drainage Board, at cost ..	5,425	19	9			
Rural Bank of N.S.W., at cost ..	2,172	15	0			
Inscribed Stock:						
Metropolitan Water, Sewerage and Drainage Board, at cost ..	1,005	0	0			
Loans on Mortgage	11,950	0	0			
				50,403	14	9
Current Assets—						
Commonwealth Savings Bank				310	4	2
				£50,713	**18**	**11**

INCOME ACCOUNT. Year Ended 28th February, 1947.

	£	s.	d.		£	s.	d.
To Salaries of Linnean Macleay Fellows	800	0	0	By Interest	1,912	9	0
,, Balance, being Surplus Income transferred to							
General Account	312	9	0				
,, Capital Account	800	0	0				
	£1,912	**9**	**0**		**£1,912**	**9**	**0**

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1947, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1947, as shown by the books. Certificates of the investments have been inspected.

S. J. RAYMENT, Chartered Accountant (Aust.), Auditor.

Sydney, 12th March, 1947.

A. B. WALKOM, Hon. Treasurer

4th March, 1947.

BACTERIOLOGY ACCOUNT.

BALANCE SHEET at 28th February, 1947.

LIABILITIES.	£	s.	d.	ASSETS.	£	s.	d.
Accumulated Funds—				Fixed Assets—			
Amount bequeathed by Sir William Macleay	12,000	0	0	Commonwealth Loans, at cost	16,320	0	0
Accumulated Income Capitalized	3,820	0	0	Current Assets—			
				Commercial Banking Company of Sydney Ltd.	124	9	6
	15,820	0	0	Commonwealth Savings Bank	818	16	7
Income Account at 28th February, 1947	1,449	6	1	Cash in hand	6	0	0
	£17,269	6	1		£17,269	6	1

INCOME ACCOUNT. Year Ended 28th February, 1947.

	£	s.	d.		£	s.	d.
To Salary	600	0	0	By Balance from 1945—46	1,421	9	4
„ Expenses		16	11	„ Interest	630	3	9
„ Petty Cash	1	10	1				
„ Balance to 1947—48	1,449	6	1				
	£2,051	13	1		£2,051	13	1

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 28th February, 1947, and certify that the above Balance Sheet and accompanying Income Account are correct and in accordance therewith, and in my opinion present the true state of the Society's affairs at 28th February, 1947, as shown by the books. Certificates of the investments have been inspected.

S. J. RAYMENT, Chartered Accountant (Aust.),
Auditor.

Sydney, 12th March, 1947.

A. B. WALKOM,
Hon. Treasurer.

4th March, 1947.

ABSTRACT OF PROCEEDINGS.

ORDINARY MONTHLY MEETING.

26th MARCH, 1947.

Dr. G. D. Osborne, President, occupied the Chair.

The Donations and Exchanges received since the previous Monthly Meeting (27th November, 1946), amounting to 22 Volumes, 408 Parts or Numbers, 13 Bulletins, 5 Reports and 23 Pamphlets, received from 65 Societies and Institutions and 2 private donors, were laid upon the table.

PAPERS READ.

1. The Influence of Molybdenum and Vanadium on Nitrogen Fixation by *Clostridium butyricum* and Related Organisms. By H. L. Jensen, Macleay Bacteriologist to the Society, and Donald Spencer, B.Sc.

2. Bryozoa from the Lower Carboniferous of New South Wales and Queensland. By Joan Crockford, M.Sc.

ORDINARY MONTHLY MEETING.

30th APRIL, 1947.

Dr. G. D. Osborne, President, occupied the Chair.

The President announced that the Council had elected Dr. A. B. Walkom to be Honorary Treasurer for the Session 1947-48.

The President also announced that the Council had elected Mr. E. Le G. Troughton, Dr. W. R. Browne, Dr. Ida A. Brown and Mr. A. R. Woodhill to be Vice-Presidents for the Session 1947-48.

The President referred to the death of Mr. Ralph Ellis of the University of Kansas, who had been a life member of the Society since 1932.

The President, on behalf of members, offered congratulations to Dr. H. L. Jensen, Macleay Bacteriologist, on his appointment to the position of Chief of the Division of Bacteriology of the State Laboratory of Plant Culture, Danish Ministry of Agriculture. Dr. Jensen's resignation has been accepted by the Council, and it is expected that he will leave for Denmark at the end of September.

Mr. T. O. Browning, Sydney; Mr. S. H. Christian, Port Moresby, Papua; Miss Janet E. Harker, B.Sc., Armidale, N.S.W.; Mr. D. L. W. Henderson, L.S., M.I.S., Woodford, N.S.W.; Mr. B. McMillan, Hamilton, N.S.W.; Miss Helen M. McRoberts, B.Sc., Lindfield, and Miss Beryl Scott, B.Sc., North Sydney, were elected Ordinary Members of the Society.

The Donations and Exchanges received since the previous Monthly Meeting (26th March, 1947), amounting to 45 Volumes, 113 Parts or Numbers, 6 Bulletins, 3 Reports and 1 Pamphlet, received from 37 Societies and Institutions and 3 private donors, were laid upon the table.

PAPERS READ.

1. Reptiles occurring above the Winter Snowline at Mt. Kosciusko. By Stephen J. Copland, B.Sc.

2. The Utilization of Fumarate and Malate by *Escherichia coli* in the presence of Molecular Hydrogen. By June Lascelles, Linnean Macleay Fellow of the Society in Biochemistry, and J. L. Still.

3. Notes on Australian Mosquitoes (Diptera, Culicidae). Part vii. The Genus *Harpagomyia*. By R. H. Wharton, B.Sc.

BRYOZOA FROM THE LOWER CARBONIFEROUS OF NEW SOUTH WALES AND QUEENSLAND.

By Joan Crockford, M.Sc.*

(Plates i–vi; fifty-one Text-figures.)

[Read 26th March, 1947.]

INTRODUCTION.

Bryozoa from widely separated areas in which marine Lower Carboniferous strata occur in eastern Australia are described in this paper; the specimens described in Part i are from the Lion Creek Limestone near Stanwell, from two horizons in the Viséan near Mundubbera, and from Cannindah in southern Queensland, and those described in Part ii are from the marine Burindi Series and also from a marine intercalation in the freshwater Lower Kuttung Series which overlies it in the Clarencetown–Paterson–Rouchel Brook district to the north of the Hunter River and from the Upper Burindi Series at Taree in New South Wales. The faunas so far known (they are probably far from complete) in these areas contain the largest and best preserved series of Bryozoa at present known from the Lower Carboniferous in eastern Australia; Bryozoa occur at many other localities from which very little collecting has so far been done, and it is certain that in time the number of genera and species described from the Lower Carboniferous here will be vastly increased.

Although many records of the occurrence of Bryozoa in rocks which are, or may be, of Lower Carboniferous age in both New South Wales and Queensland have hitherto been made, only a few of these records are accompanied by descriptions or by figures, and the localities from which they have been collected are usually not at all precisely recorded. The more important of these previous records are discussed in this paper.

Both in New South Wales and in Queensland, despite the comparatively small number of species so far described, the cosmopolitan nature of the Lower Carboniferous bryozoan faunas compared with the limited number of families and genera present in the Permian is very striking. The Permian throughout eastern Australia contains enormous numbers of fenestellids and stenoporids, but Bryozoa belonging to other families are extremely rare, although a few Rhabdomesontidae and Acanthocladiidae do occur. In the Lower Carboniferous, on the other hand, although fenestellids are abundant, stenoporids are virtually absent—the earliest definitely known stenoporid in Australia is a specimen from the Upper Viséan Lion Creek Limestone at Stanwell; but many other bryozoan genera, belonging to the Fistuliporidae, Sulcoreteporidae, Rhabdomesontidae and Acanthocladiidae, are well represented; the cosmopolitan nature of the fauna is strongly emphasized by the occurrence here of specialized and comparatively rare genera, such as *Evactinopora*, *Archimedes*, *Goniocladia* and *Ramipora*, particularly as these first appear in Australia upon an horizon approximately equivalent to that in which they first occur in other parts of the world.

The stratigraphic significance of these Bryozoa and the relationship of these Lower Carboniferous faunas to those occurring in later Upper Palaeozoic rocks in Australia are to be discussed in detail in a later paper.

Dr. Dorothy Hill and Dr. F. W. Whitehouse of the University of Queensland kindly lent me specimens from Mundubbera which contain Bryozoa previously exhibited by Dr. Whitehouse at a meeting of the Royal Society of Queensland; specimens which Mr. R. Etheridge, jnr., described from the Lion Creek limestone at Stanwell were lent to me from the Australian Museum Collections. I am indebted to Dr. G. D. Osborne for many

B

specimens of Bryozoa which he has collected for me from the Burindi and Lower Kuttung Series in the northern Hunter River district. Dr. Ida Brown has also collected a number of specimens for me from more northerly outcrops of the Burindi Series, and has been generous with her helpful criticism during the writing of this paper.

PART I.   LOWER CARBONIFEROUS BRYOZOA FROM QUEENSLAND.

Fossiliferous marine strata of Lower Carboniferous age outcrop at a large number of localities in Queensland, but there are very few records of the occurrence of Bryozoa in rocks which are of undoubted Lower Carboniferous age. This is partly due to the fact that most of the localities given in early descriptions and lists of fossils were very generalized, and even the approximate horizon from which the fossils were collected is made uncertain by the presence in the same general area of Devonian or of Upper Carboniferous or Permian fossiliferous rocks. The older records, therefore, are of little value, with the exception of the interesting record by Etheridge (1900, 8) of the occurrence of "*Fistulipora* or *Hexagonella*" and "*Stenopora Leichardtii*" from the Oolitic Limestone of Lion Creek, Stanwell, near Rockhampton; these specimens, now in the Australian Museum Collection, are re-described in this paper; Etheridge's paper is of particular interest in that it records the earliest stenoporid so far known with certainty to occur in Australia.

In 1929 Dr. F. W. Whitehouse exhibited at a meeting of the Royal Society of Queensland specimens of *Archimedes* and *Evactinopora* collected from strata of Viséan age near Mundubbera in Queensland. The two specimens of *Archimedes* were collected from the Riverleigh Limestone, the age of which has been determined from the coral fauna [described in detail by Hill (1934, 105; 1943, 62)] to be Upper Viséan or possibly slightly younger. The specimen of *Evactinopora* was collected from an oolitic limestone horizon in the same district; this limestone, which contains *Palaeacis* sp. cf. *cuneiformis* Halme (Hill, 1934, 101) is probably slightly younger in age than the Riverleigh limestone. The fossils contained in all of these specimens were silicified, and when they were etched, specimens of a number of other interesting species of Bryozoa were found to be contained in them; these forms, as well as the species of *Archimedes* and *Evactinopora*, are described in this paper.

Specimens of limestone which Professor S. W. Carey collected from the Lower Carboniferous limestones at Canindah, to the south of Mundubbera (6448, Sydney Univ. Colln.), also contain silicified fistuliporoids.

No Bryozoa from the younger Carboniferous rocks of Queensland are described in this paper, but they form an abundant part of the fauna of the Neerkol Series of Upper Carboniferous age in the type locality for this Series, near Rockhampton, and in other districts.

The full localities from which the Lower Carboniferous Bryozoa from Queensland described in this paper were collected are as follows:

Canindah: A crinoidal limestone horizon, Old Canindah Homestead, near Monto, Queensland (= loc. "a" of Hill, 1934, 106).

Lion Creek Limestone: Oolitic Limestone horizon in Lion Creek, Stanwell, near Rockhampton.

Oolitic Limestone, Par. Mundowran: Oolitic Limestone horizon in Por. 193, Par. Mundowran, Co. Yarrol, near Mundubbera.

Riverleigh Limestone: Latza's Farm, Pors. 21 and 22, Par. Malmoe, Co. Yarrol, near Mundubbera.

The coral faunas of these limestone horizons have been described and their stratigraphic position discussed by Hill (1934, 1943) and work on them summarized also by Bryan and Jones (1944).

DESCRIPTION OF SPECIES.
Order CYCLOSTOMATA Busk.
Family FISTULIPORIDAE Ulrich.

Fistuliporidae Ulrich, 1882; Cheilotrypidae Moore and Dudley, 1944, 255.

Nomenclature of this family and of several genera within it has been discussed at length by Moore and Dudley; they consider the generic name *Fistulipora* M'Coy a

homonym and the name Fistuliporidae therefore not available for this family; they propose to substitute the name Cheilotrypidae (type genus: *Cheilotrypa* Ulrich, 1884).

According to Moore and Dudley, *Fistulipora* M'Coy, 1850, is a homonym of *Fistulipora* Rafinesque, 1831, the name having been used by Rafinesque for an unrecognizable Palaeozoic fossil; this genus, despite the fact that it cannot now be identified, was, as Moore and Dudley point out, validly designated, and should therefore, provided the name was published by Rafinesque prior to M'Coy's paper in 1850, render *Fistulipora* M'Coy a homonym. Whether Rafinesque actually did publish this name prior to 1850, however, seems to be open to question; Moore and Dudley state (p. 253) that "Rafinesque (1831, p. 5) published *Fistulipora* as the name of a Paleozoic fossil from Kentucky, antedating McCoy's paper by some 18 years", but in their bibliography (p. 310) the reference to this paper is given as follows:

"Rafinesque, C. S., *1831*, Description of fossils in cabinet, pp. 1–5, Philadelphia (private publication)."

I have been unable to find any other reference to this paper by Rafinesque, and I am therefore in no position to discuss fully the status of this publication. If, however, this reference is to a descriptive catalogue of a similar type to a museum catalogue and was not actually published by Rafinesque in 1831, in the sense in which the term "publication" may be interpreted in the Rules of Nomenclature (cf., discussion of this term by Stiles, 1928, 571–578), as seems to me rather probable from the manner in which Moore and Dudley refer to this paper as a "private publication", *Fistulipora* Rafinesque would rank as a manuscript name, and when published *fide* Rafinesque by a later author should take the date of this later reference, this being the date of actual publication of the name; in this case, the date of publication of *Fistulipora* Rafinesque should be either 1864, in which year Binney and Tryon published a work entitled "The complete works of Constantin Smaltz Rafinesque" in which I presume this 1831 paper would have been included (Binney and Tryon's paper is not available to me), or else 1944, when Moore and Dudley reprinted Rafinesque's definition of this name. In either of these cases, *Fistulipora* M'Coy, 1850, would have clear priority over *Fistulipora* Rafinesque.

This interpretation of the question, under which *Fistulipora* M'Coy is considered to be a valid name, is followed here, and the name Fistuliporidae is therefore used for the family.

Three sub-families within the Fistuliporidae are recognized in this paper. As is more fully discussed after the diagnoses of the sub-families Hexagonellinae, n. sub-fam., and Goniocladiinae Waagen and Pichl, it is here considered that a number of genera previously referred to the Sulcoreteporidae are essentially fistuliporoid in their internal structure; the absence of structures diagnostic of *Sulcoretepora* and closely related genera in their internal structure serves clearly to differentiate these genera from true Sulcoreteporidae, which in some cases they fairly closely resemble externally. These genera therefore appear more logically referred to the Fistuliporidae than to the Sulcoreteporidae, and are here placed in two sub-families within this family; typical Fistuliporidae are therefore referred to a third sub-family, the sub-family Fistuliporinae Waagen and Wentzel.

Sub-family FISTULIPORINAE Waagen and Wentzel, 1886 (emend.).

Fistuliporinae Waagen and Wentzel, 1886, 909.

Typical Fistuliporidae, with massive, laminar, encrusting, or ramose zoaria; surface with monticules or maculae; zooecial tubes usually with well-developed lunaria, and with or without diaphragms; tubes separated by vesicular tissue, which is sometimes separated by dense tissue as the surface is approached.

This sub-family was originally proposed by Waagen and Wentzel in their monograph on the Salt Range Fossils to include two of the genera with which they were dealing, *Fistulipora* M'Coy and *Dybowskiella* Waagen and Wentzel. It is regarded in this paper as including all the genera of Fistuliporidae which are not referred to the sub-families Hexagonellinae, n. sub-fam., and Goniocladiinae Waagen and Pichl, and therefore to

include all the genera listed as belonging to the Fistuliporidae by Bassler in 1935 (p. 16) except *Hexagonella* Waagen and Wentzel and *Meekopora* Ulrich.

Genus FISTULIPORA M'Coy, 1850.

Fistulipora M'Coy, 1850, 131; *Fistulipora* M'Coy, Ulrich, 1890, 382, 474; *Fistulipora* (pars) M'Coy, Bassler, 1929, 41; Crockford, 1944, 143. [non] *Fistulipora* Rafinesque, Moore and Dudley, 1944, 253.

Zoarium incrusting to massive or ramose, surface with monticules or maculae composed of aggregations of vesicles or of enlarged zooecia; zooecial tubes with inconspicuous or faint lunaria, or with thickened lunaria the ends of which do not indent the zooecial tubes; diaphragms usually developed; interzooecial spaces occupied by vesicular tissue which is sometimes replaced by dense tissue near the surface.

Genotype: *Fistulipora minor* M'Coy, 1850.

Range: Ordovician to Permian.

The status of this generic name has been referred to in discussion of the naming of the family Fistuliporidae (pp. 2–3), and it has been pointed out that, since the paper in which Rafinesque proposed the generic name *Fistulipora* for an unknown Palaeozoic fossil was a private publication, and the name does not appear to have been actually published prior to 1850, *Fistulipora* M'Coy, 1850, appears to be the valid name for this genus of bryozoans.

The generic name *Fistulipora* has until recently been used to include incrusting, massive and ramose zoaria with typical fistuliporoid internal structure, irrespective of the degree of development of the lunaria. From recent work, and especially from that of Moore and Dudley (1944), it appears that subdivision of the genus upon the basis of lunarial development is possible and will become essential as work on this group progresses. *Fistulipora* ranges from the early Ordovician to the Permian, and within the many species grouped under this name great variation in the size, thickening, and degree of development of the lunarium is found. Moore and Dudley, working upon the assumption that *Fistulipora* was not a valid name, considered that *Cyclotrypa* Ulrich, 1896, proposed for species in which lunaria are absent or inconspicuous, should be used for species in which the lunaria are poorly developed. The genotype of *Fistulipora*, *F. minor* M'Coy, 1850 (? = *Calamopora incrustans* Phillips), is in need of revision from type or topotype material, but appears from M'Coy's original illustrations to have been a species in which the lunarium was either poorly developed or almost absent, and species which have been closely compared with this form by later workers upon Carboniferous material from the British Isles have always been species in which the lunaria are inconspicuous. *Fistulipora minor* at present therefore appears to belong to the group for which *Cyclotrypa* was later proposed, and *Cyclotrypa* must therefore be considered a synonym of *Fistulipora*, unless a re-examination of the type of *F. minor* or of topotype material shows differences between them.

One group of species common in Upper Palaeozoic rocks is differentiated from *F. minor* and closely-related species by the possession of very strong lunaria, the ends of which indent the zooecial tubes so that they are bilobate or trilobate in transverse section; these forms are referred to *Dybowskiella* Waagen and Wentzel, 1886. There are many species, however, in which the lunaria are strongly thickened but do not at all project into the zooecial tubes, which lack the strongly-marked lobed appearance of the tubes of *Dybowskiella*. Many of the species of *Fistulipora* which have been described from the Permian of Timor and of Western Australia belong to this group; these seem at present best still referred to *Fistulipora*.

As well as these differences in the degree of development of the lunarium, many species both of *Fistulipora* and of *Dybowskiella*, and particularly late Palaeozoic forms, show progressive replacement of the vesicular tissue near the surface by dense tissue; this characteristic, which appears to be of specific and not of generic value, is found in several of the fistuliporoids in the Western Australian Permian, and occurs to a slight degree in both of the species of *Dybowskiella* described in this paper.

FISTULIPORA ETHERIDGEI, n. sp. Text-figs. 1, 2.

Fistulipora or *Hexagonella*, Etheridge, 1900, 8.

Holotype: F.6856C, Australian Museum Colln.

Horizon and locality: Lion Creek Oolitic Limestone, Stanwell, near Rockhampton.

Laminar Fistulipora; *zooecial tubes very slightly indented by thin lunaria; diaphragms numerous and closely spaced; tubes separated by coarse vesicular tissue.*

The zoaria consist of thin sub-circular laminar expansions up to 10 mm., but usually about 3 mm. in their greatest thickness and 2·5 cm. or more in diameter; individual colonies are frequently built up, especially in the case of the thicker zoaria, by thin discontinuous laminae; Etheridge commented upon this lamination and considered it a possibility that the zoaria were bifoliate, but the direction of growth of the zooecia shows clearly that these are successive laminae and not the two sides of a bifoliate colony. The base of the colony was covered by an undulating and concentrically wrinkled epitheca, shown very well on the etched under surface of one of the colonies; the upper surface of the zoarium is irregular but is more or less flattened. Small slightly depressed spot-like maculae about 1·5 to 2 mm. in diameter are developed on the upper surface 3·5 to 5 mm. apart; these maculae are composed of aggregations of vesicular tissue, but their surface, like the surface between the apertures, appears solid except where it has been weathered sufficiently to reveal the vesicles.

The zooecia are tubular; their apertures are almost imperceptibly indented by the development of slight lunaria, which extend around rather more than one-quarter of the circumference of each tube; these lunaria are a little raised at the surface. The tubes are usually from 0·19 to 0·24 mm. in diameter, but some of the tubes adjacent to maculae are considerably larger, up to 0·32 mm. in diameter; the lunaria are inconspicuous and unthickened in sections, and do not show out as well as they do on etched surfaces. The zooecia are prostrate for a very short distance along the basal epitheca and then bend upwards to the surface. Numerous thin, slightly concave, complete diaphragms are developed in the zooecial tubes; as many as seven or eight of these diaphragms may occur in 1 mm., but the tubes are usually without diaphragms for a short distance from the surface, about 0·5 to 0·9 mm., though occasionally diaphragms are developed almost until the surface is reached; in some cases where the laminae are very thin, less than 1 mm. in thickness, no diaphragms have been developed in some of the zooecial tubes. The zooecia are separated by rather coarse vesicular tissue, a single row of which usually occurs between adjacent zooecia. A very thin layer of dense tissue was developed at the surface. In 7 sq. mm., excluding maculae, there are about 30 zooecial tubes.

Etheridge hesitated between the generic names *Hexagonella* and *Fistulipora* for this species, as he considered it possible that the zoarium might have been bifoliate; however, the zoaria are composed of successive laminae growing in the same direction and not of two laminae growing together back to back, and therefore the species cannot be referred to *Hexagonella*. The thin laminar growth form, the poorly-developed lunaria, and the coarse vesicular tissue readily serve to distinguish this species.

Genus DYBOWSKIELLA Waagen and Wentzel, 1886.

Dybowskiella Waagen and Wentzel, 1886, 910, 916. Synonym: *Triphyllotrypa* Moore and Dudley, 1944, 260, 291.

Zoaria laminar, massive, lobate or coarsely ramose, with fistuliporoid internal structure but differing from Fistulipora *in possessing very strongly-developed lunaria, the ends of which project into the zooecial tubes, which are therefore bilobate or trilobate in transverse section; typically the projecting ends of the lunaria form longitudinal ridges, termed pseudosepta, within the zooecial tubes.*

Genotype: *Dybowskiella grandis* Waagen and Wentzel, 1886 (as lectotype of this species, of which a number of specimens from different localities was originally figured without selection of a holotype, the specimen figured by Waagen and Wentzel, 1886, on Pl. civ, figs. 2a and 2b, is here selected; the locality of this specimen is Upper Productus Limestone, from the mountains east of Katwáhi).

Range: Devonian to Permian.

Moore and Dudley considered that the genotype of *Dybowskiella* possessed a hollow ramose zoarium, and they therefore proposed the genus *Triphyllotrypa* for species with similar internal structure but with laminar, massive or lobate zoaria. Waagen and Wentzel (1886, Pls. cii, ciii, civ, figs. 1–4, 7; cvi, fig. 7; cxv, fig. 6) published numerous figures of *Dybowskiella grandis*, the genotype of *Dybowskiella*, and while a number of these shows ramose branches with an irregular central cavity which they attributed partly to the zoarium having incrusted some irregular soft body or to worm borings, and whose marked irregularity does not suggest close comparison with the central tubes shown in *Coelocaulis*, *Cheilotrypa* and *Rhabdomeson*, two illustrations (Pl. civ, fig. 2b. and Pl. cvi, fig. 7) show ramose branches which are solid and have no suggestion of a central cavity. In other specimens, which Waagen and Wentzel figure, the central cavity may be fortuitous and due to breaking down of the looser tissue of the central part of the branch so that the central part of the zoarium was later filled by sediment, an irregularity of preservation frequently found in the central part of a coarse ramose bryozoan colony. The specimen illustrated by Waagen and Wentzel, and here selected as lectotype, of *Dybowskiella grandis* possesses a solid ramose zoarium.

Triphyllotrypa Moore and Dudley differs from *Dybowskiella* only in the form of its zoarium, this being a laminar expansion in the type of *Triphyllotrypa* and laminar, massive, and in one case lobate, in other species referred to this genus. The zoarial difference alone between incrusting, laminar, massive and solid ramose growth forms in the fistuliporoids does not appear to be a character of generic significance; the zoarial form of many species, such as *Triphyllotrypa spissa* Moore and Dudley, where the upper surface of an incrusting zoarium "bears local upward projections, one of them 16 mm. high", provides evidence of gradation between these different types of zoaria. No structural internal differences exist between *Dybowskiella* and *Triphyllotrypa*. It is here considered therefore that *Triphyllotrypa* must be regarded as a synonym of *Dybowskiella*.

No structures which could serve to differentiate generically the two Lower Carboniferous species described in this paper from Queensland and New South Wales from Permian species described by Waagen and Wentzel and by Moore and Dudley or from species from the Permian of Timor, Western Australia and the Northern Territory, which should be referred to this genus, could be found. Prominent trilobate zooecia are found also in some Devonian species, e.g., *Fistulipora foordi* Ulrich, 1890, and *F. triloba* Hall and Simpson, 1887.

<center>DYBOWSKIELLA CRESCENTICA, n. sp. Text-fig. 3.</center>

Holotype: 6448, Sydney Univ. Colln.

Horizon and locality: Crinoidal Limestone, Old Cannindah Homestead, near Monto, Queensland.

Incrusting Dybowskiella; zoarium thin, zooecial tubes with pronounced lunaria, the ends of which are projecting; tubes short, usually without diaphragms, and separated by coarse vesicular tissue.

The zoarium is incrusting; it is thin, usually about 0·08 to 1 mm. but sometimes slightly more in thickness; the holotype encrusts a thick crinoid stem and from one side of it a hollow spherical outgrowth, apparently originally encrusting, but whose support is now worn away, is shown in thin section. A thin epitheca is developed on the lower side of the zoarium; on the upper surface spot-like raised maculae about 1 mm. in diameter and 4 mm. apart are developed; these maculae are composed of aggregations of vesicular tissue. Each zooecial aperture is placed in the centre of a polygonal depressed area, the junction of the edges of these areas forming prominent polygonal ridges on the surface; the apertures are strongly indented by lunaria, but these lunaria are only slightly raised at the surface.

The zooecial tubes are short, being horizontal for a short distance and then bending outwards sharply to the surface. They are strongly indented by thick horse-shoe shaped lunaria, which extend around about one-half of the circumference of each tube; the measurements of the tubes are: *a*, 0·24 to 0·29 mm.; *b*, 0·22 to 0·27 mm.; *c*, 0·14 to

0·19 mm.; d, 0·15 to 0·19 mm.* The lunaria are considerably thickened and are very prominent in sections. An occasional diaphragm is developed in some of the zooecial tubes, but most of the tubes are without diaphragms. The zooecia are separated by rather flattened coarse vesicles, two rows of which are usually developed between adjacent zooecia; in some places these vesicles are noticeably thick walled and have become partially replaced by dense tissue. There were about 26 zooecia in 7 sq. mm.

The form of the zoarium, raised maculae, and very prominent lunaria readily serve to distinguish this species from *Fistulipora etheridgei*, n. sp.

Sub-family HEXAGONELLINAE, n. sub-fam.

Zoaria bifoliate, consisting of two or more layers of zooecia grown together back to back; where three or more layers of zooecia are developed vertical-rayed growth-forms are formed; margins of the zoarium sharp or rounded, and with a narrow non-poriferous border; surface, except where the zoarium is very narrow, with non-celluliferous maculae, characteristic for each species in their size, shape and spacing; fine ridges which divide the surface into areas of characteristic size and shape also developed in many species. Zooecia tubular, lying parallel to the mesial lamina for some distance, usually about one-third their length or less, then bending fairly rapidly upwards to meet the surface almost perpendicularly. Tubes rounded, not angular, in cross-section, and with lunaria poorly developed or absent; without hemisepta, but frequently with complete diaphragms. Mesial lamina with fine median tubuli. Zooecia separated internally by vesicular tissue, and never arranged between vertical double plates; vesicles replaced by dense tissue as the surface is approached.

Range: Mississippian to Permian.

The genera which are here considered to belong to this sub-family are:

Coscinium Keyserling, 1846; *Evactinopora* Meek and Worthen, 1865; *Glyptopora* Ulrich, 1884; *Hexagonella* Waagen and Wentzel, 1886; *Meekopora* Ulrich, 1889; *Meekoporella* Moore and Dudley, 1944; *Prismopora* Hall, 1883; and *Fistulamina*, n. gen.

Other genera, such as *Scalaripora* Hall, 1883, may also possess the same type of internal structure as *Hexagonella*, and if so, should be referred here.

The sub-family Hexagonellinae includes genera which, with the exception of *Hexagonella*, *Meekopora* and *Meekoporella*, have previously been referred to the family Sulcoreteporidae Bassler (= Cystodictyonidae Ulrich), but do not show the internal structure characteristic of *Sulcoretepora*. *Sulcoretepora* itself and a number of genera closely related to it show a specialized type of internal structure, the zooecia on each side of the mesial lamina being arranged in rows between longitudinal vertical plates, and the zooecia are rather short, semi-cordate in outline and sharply geniculate, with well-developed hemisepta. These genera are typical members of the Cryptostomata. Other genera previously referred to the family, however, show fistuliporoid internal structure, identical with the type of internal structure found in *Hexagonella*; *Hexagonella* differs from *Fistulipora* principally in the bifoliate form of its zoaria, and also in the typically weak development or absence of lunaria. As a group, the genera here referred to the Hexagonellinae are also characterized by rather more strongly geniculate zooecia than those of typical fistuliporoids.

It has long been recognized that close similarity exists between some genera referred to the Sulcoreteporidae and the Fistuliporidae; indeed, Ulrich, in his original discussion of the family Sulcoreteporidae (as Cystodictyonidae Ulrich, 1885, 35), pointed out the close relationship of the group of genera which he included in this family to the Fistuliporidae, stating that they differed from it "mainly in possessing two or more leaved zoaria, the margins of which are non-poriferous and usually sharp". In spite of this long recognized relationship, these genera have been classified in different orders, those placed in the Fistuliporidae in the Cyclostomata, and those placed in the Sulcoreteporidae in the Cryptostomata. Had the genera in which this close relationship is shown been of early Palaeozoic age, their classification into different orders might perhaps be accounted for as the result of imperfect differentiation of two separate

---

* Measured as previously explained (Crockford, 1944, 142, Text-fig. C).

phylogenetic groups at an early stage of their evolution, but with Bryozoa of Carboniferous to Permian age it should be possible readily to differentiate between genera of two orders which were distinct in the early part of the Ordovician. It is here considered that such differentiation can be clearly and easily made if the Sulcoreteporidae are restricted to genera showing the very specialized type of cryptostomatous internal structure shown in *Sulcoretepora*, and the genera with fistuliporoid internal structure which constitute the remainder of this family as hitherto defined are removed and classified with *Hexagonella*.

Since bifoliate zoaria are developed in such a large group of genera with fistuliporoid internal structure, and these bifoliate zoaria are elaborated into so many diverse and specialized growth-forms, such as those found in *Evactinopora*, *Coscinium* and *Glyptopora*, it is here considered that they form a compact and phylogenetically related group within the Fistuliporidae which should be classified as a separate sub-family.

Genus EVACTINOPORA Meek and Worthen, 1865.

Evactinopora Meek and Worthen, 1865, 165; *Evactinopora* Meek and Worthen, Ulrich, 1884, 42; Ulrich, 1890, 387, 508.

Zoarium free, consisting of three or more bifoliate vertical leaves, radiating from an imaginary axis so as to present a star-shaped outline in transverse section; zooecia and internal structure as in Hexagonella.

Genotype: *Evactinopora radiata* Meek and Worthen, 1865.

Range: Mississippian to Permian.

EVACTINOPORA IRREGULARIS, n. sp.   Pl. 1, figs. 3–6; Text-figs. 4–6.

Evactinopora, Whitehouse, 1929, xii; Hill, 1934, 105.

Holotype: F.5769A, Univ. Queensland Colln.

Horizon and locality: Oolitic Limestone, Por. 193, Par. Mundowran.

Four-rayed Evactinopora; *rays bifoliate, thin, broad, leaf-like; surface with small, solid, regularly placed maculae; zooecia placed back to back along the mesial lamina in the centre of each branch, where they are separated by fine vesicular tissue, and then bending rapidly outwards to meet the surface at right angles, being separated in the outer part of the zoarium by dense tissue.*

The zoarium is bifoliate, the growth-form being four-rayed; the holotype is a broken specimen, and is now 5·5 cm. high and about 5 cm. in its greatest diameter, neither of these measurements being the full extent of the perfect zoarium. The rays intersect at the base of the zoarium at about 80° to 85°, one of the rays being curved and the others more or less straight; at the upper end, however, two of the rays have curved away from each other, the zoarium here being shaped like a bent H (Pl. 1, fig. 4). The best preserved ray reaches a maximum width of 3·7 cm., its outer edge being blunt and rounded. Small, solid, slightly depressed maculae are prominent on the surface of the rays; the maculae are elongated, 2·8 to 4 mm. long and about 1 mm. wide, and they are arranged rather regularly in close-spaced rows radiating gradually from the base of the colony; these rows of maculae are usually almost vertical near the centre of the zoarium, and curve outwards obliquely near the edges of the rays, but on one of the rays all of the rows of maculae are oblique; the centres of the maculae are usually placed from 4·5 to 7 mm. apart. The zooecial apertures are small, and are rounded to slightly oval, 0·16 to 0·22 × 0·16 mm. in diameter; they are slightly indented by the lunaria, which, when well preserved, are raised and hood-like at the surface; the apertures show up clearly on the etched and weathered surface of the zoarium, the tissue between them being solid at the surface. On the broken edges of the rays the mesial lamina and longitudinal sections of the zooecial tubes can also be seen very clearly.

The zooecia are tubular; they arise on each side of a distinct mesial lamina, along which they are horizontal for a short distance (up to 0·7 mm.) and then curve rapidly upwards to meet the surface at about 75° to 90°. In transverse section the tubes are rounded, or they may be a little indented by a slight lunarium where the tube wall is curved to a slightly shorter radius around about one-third of the circumference of the
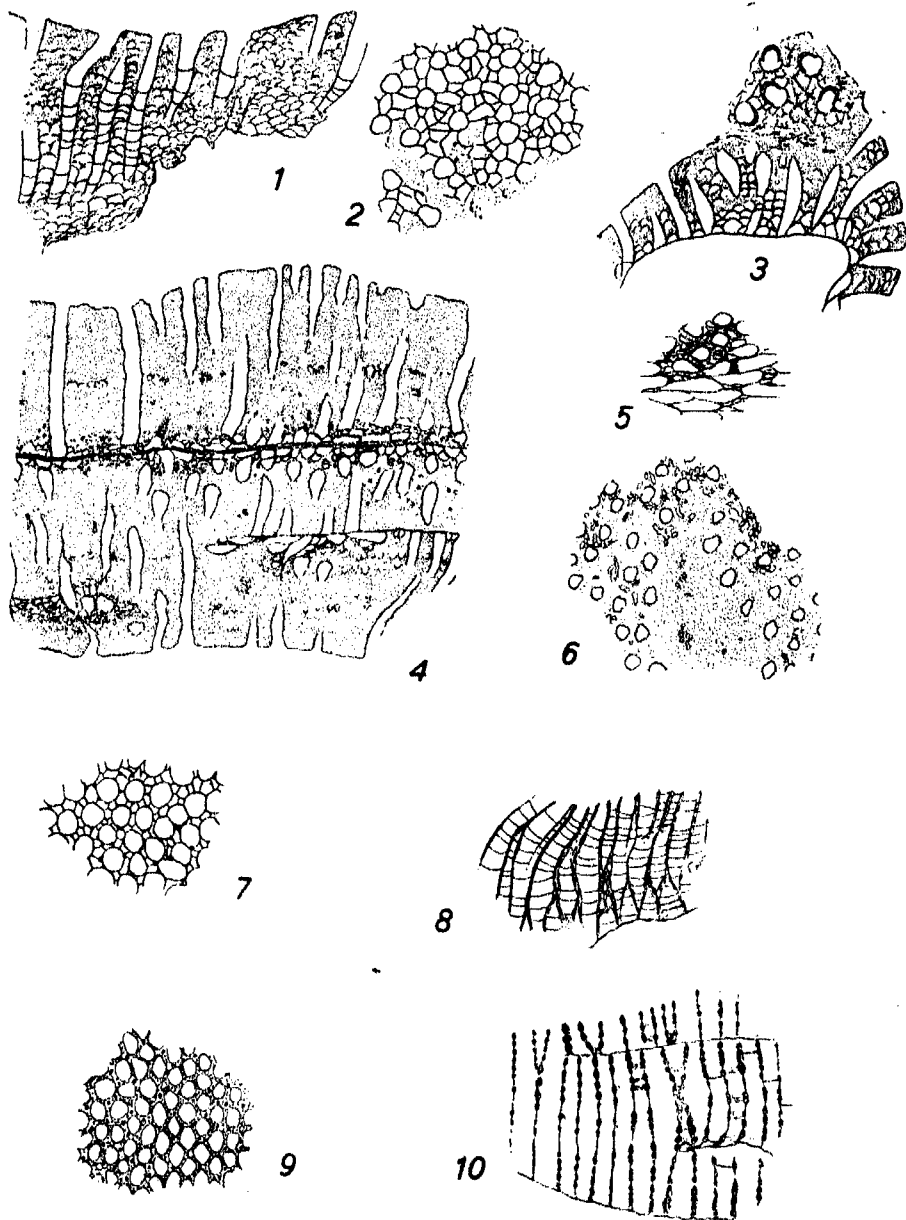
Text-figs. 1-2.—*Fistulipora etheridgei*, n. sp., × 10. 1. Vertical section of the holotype. 2. Tangential section of a second specimen in the same piece of limestone. (Slides 131A-D, Australian Museum Colln.)

Text-fig. 3.—*Dybowskiella crescentica*, n. sp., × 10. Oblique section of the holotype.

Text-figs. 4-6.—*Evactinopora irregularis*, n. sp., × 10. 4. Vertical section through one ray of the holotype. 5. Tangential section through a ray of the holotype, the section being cut adjacent to the mesial lamina upon which the zooecial tubes are recumbent for a short distance before they bend upwards to the surface. 6. Tangential section cut close to the surface of the holotype.

Text-figs. 7-8.—*Leioclema porosa*, n. sp., × 10. 7. Tangential section of the holotype. 8. Vertical section of a second specimen in the same piece of limestone. (Slides 131A-D, Australian Museum Colln.)

Text-figs. 9-10.—*Stenodiscus stanwellensis*, n. sp., × 10. 9. Tangential section of the holotype. 10. Vertical section of a second specimen in the same piece of limestone. (Slides 131A-D, Australian Museum Colln.)

tube; the silicification of the specimen has made these lunaria rather difficult to observe, but they are shown quite clearly in some of the tubes by slight thickening of the tube wall, and by their different curvature. In the central part of the zoarium the tubes are separated by small vesicles, but these are rapidly replaced by dense tissue, with only occasional vesicles, as the tubes bend upwards to the surface; where the growth of the zoarium has been interrupted and rejuvenation has occurred, narrow zones of these vesicles are found closer to the surface, in places associated with rejuvenated zooecial tubes. No diaphragms and no hemisepta occur in the tubes, and acanthopores are not developed. Ulrich (1884, 42) stresses the degree to which the apertures in the early part of the zoarium have been infilled and the zoarium itself thickened by calcareous tissue in *E. radiata*; although the lower part of the zoarium has been thickened by over-growths of vesicles and dense tissue and by rejuvenation of the zooecia in this specimen of *E. irregularis*, the apertures are not infilled by the dense tissue to any marked degree; the base of the specimen as it is now preserved appears to have been slightly spreading, and this may perhaps indicate that this species was lightly attached at the base, as was *E. trifoliata*, n. sp., from the Burindi Series in New South Wales; as a free zoarium would have evolved from an attached form, this suggests that both of these Australian Lower Carboniferous species are slightly more primitive forms than any species of *Evactinopora* hitherto described.

This species of *Evactinopora* is clearly differentiated in the details of its external structure from the five described species of this genus, four of which come from the Mississippian of the United States, and one, *E. crucialis* Hudleston, 1883, from the Permian of Western Australia (*E. dendroidea* Hudleston, 1883, is a species of *Hexagonella*).

The internal structure of the genotype, *E. radiata*, has been described and figured by Ulrich (1884, Pl. 2, figs. 1, 1 *a–c*). Ulrich's figures show the tubular zooecia arising on each side of the mesial lamina, the tubes being slightly indented by the lunaria; there are no hemisepta nor diaphragms; the zooecia are separated by vesicular tissue, replaced by dense tissue as the surface is approached; Ulrich does not mention the presence of maculae in this species, but a portion of a macula is cut on the right hand side of the section figured in his Fig. 1*b*, where a comparatively large area is devoid of zooecia and is occupied by vesicles and dense tissue. In its internal structure, there-fore, *E. irregularis* closely approaches the genotype.

<center>Genus FISTULAMINA, n. gen.*</center>

<center>FISTULAMINA MALMOENSIS, n. sp.   Pl. iii; figs. 1, 2; Text-figs. 12, 15.</center>

Holotype: F.5768E, Univ. Queensland Colln.

Horizon and locality: Riverleigh Limestone, Pors. 21 and 22, Par. Malmoe.

Broad, strap-like Fistulamina; apertures small, with distinct lunaria, and arranged in 3 to 6 rows on each surface of zoarium; non-poriferous margins of about equal thick-ness and equally sharp on each side of branch.

The zoarium is broad and flattened, bifurcating at irregular intervals, typically in the plane of the mesial lamina but occasionally at an angle to this plane; it is from 1·52 to 2·88 mm. in width, and is acutely elliptical in section, its thickness at the centre being from about 0·49 to 1·22 mm.; this thickness is greatest closer to the base of the colony, the branches tapering in thickness near their extremities. The non-poriferous margins of the branches are narrow and are of about equal width on each side; the margin is sharp on each side of the branch, and it is marked by a fine longitudinal ridge, caused by slight projection of the ends of the mesial lamina. The zooecial apertures are arranged rather regularly in longitudinal and in diagonal rows; usually there are four to six, occasionally three, rows on each surface of the zoarium. The apertures are 0·13 to 0·14 × 0·09 to 0·13 mm. in diameter; they are slightly indented by small but distinct lunaria, where about one-third of the circumference is curved to a markedly shorter radius; these lunaria are placed on the side of the aperture closest to an edge of the branch. The apertures are surrounded by slight peristomes, which are

strongly raised and hood-like on the side on which the lunaria are developed; these hoods are most marked on the lateral rows of zooecia. The centres of successive apertures are spaced 0·51 to 0·71 mm. apart, and there are about 17 apertures in 10 mm. The surface between the apertures is solid and finely granular.

The zooecia lie parallel to the mesial lamina for about 1 mm. and then bend upwards to meet the surface almost perpendicularly. They are not arranged in longitudinal rows between vertical plates, but are separated close to the mesial lamina by a few coarse vesicles and closer to the surface by dense tissue. No diaphragms occur. The internal structure is not well shown in thin section owing to silicification of the zoaria, but both in thin section and on broken edges it is seen to be similar to that shown in *Fistulamina inornata*, n. sp., rather than to the structure shown in species of *Sulcoretepora*, which it resembles externally. It is readily distinguished from *F. inornata* by the differences in their size, in the number of rows of zooecia, and the size of the apertures, and internally by the smaller number of vesicles and by the much larger size of the vesicles developed in this species.

Sub-family GONIOCLADIINAE Waagen and Pichl, 1885.

Goniocladinae* Waagen and Pichl, 1885, 775; = Goniocladiidae Nikiforova, 1938, proposed as a family of the Cryptostomata.

Bifoliate Fistuliporidae; zoaria forming narrow branches, which divide in a plane perpendicular to that of the mesial lamina and may anastomose or form pinnate or irregularly branching zoaria; mesial lamina running from the centre of the obverse to the centre of the reverse surface, and projecting slightly at each end so that both these surfaces are carinate; the carina is typically bordered on both obverse and reverse surfaces by a margin of non-celluliferous tissue, this being much wider on the reverse surface and sometimes almost obsolete on the obverse; zooecial apertures arranged in rows on each side of the carina of the obverse surface; peristomes usually strongly developed, lunaria present or absent; zooecia tubular, without hemisepta, and with diaphragms only very rarely developed; rows of zooecia never separated internally by vertical plates, but they are separated close to the mesial lamina by vesicular tissue, which is replaced by dense tissue as the surface is approached; mesial lamina with fine median tubuli.

Range: Mississippian to Permian.

Waagen and Pichl (1885, 775, 804), who regarded *Goniocladia* and *Ramipora* as members of the Fenestellidae, proposed that these two genera should be separated from the remainder of the family as the sub-family Goniocladinae. Nikiforova (in *Zoological Record*, 1938—the original publication is not available in Australia) has proposed that *Goniocladia, Ramipora, Ramiporalia, Ramiporidra, Ramiporina* and *Volgia* should be grouped together as a separate family of the Cryptostomata, the family Goniocladiidae.

Goniocladia and related genera are closely similar, in internal structure particularly, to *Hexagonella*. Like *Hexagonella*, they differ from *Sulcoretepora*, with which they were for a long time classified, in the shape of their zooecia, in the lack of hemisepta in the zooecia, and in the absence of vertical plates between the rows of zooecia; their internal structure is essentially fistuliporoid. They differ from *Fistulipora* itself in the narrow bifoliate form of their zoaria, in the weak development or absence of lunaria, and in their slightly more geniculate zooecia; like many late Palaeozoic species of *Fistulipora, Hexagonella, Evactinopora*, etc., the vesicular tissue between the zooecia is replaced by dense tissue as the surface is approached, so that the interspaces are solid at the surface. From the Hexagonellinae, these genera differ in the form of their zoaria—in the bifurcation of their branches, typically in a plane at right angles to the mesial lamina instead of in the plane of the mesial lamina, in the orientation of the zooecia towards one surface so that obverse and reverse surfaces may be distinguished, and in their anastomosing, pinnate, or irregularly pinnate, zoaria.

---

* This spelling is here regarded as a *lapsus calami*, since the sub-family name should have been formed by adding "*inae*", not "*nae*", to the stem of the generic name; it is therefore corrected here to Goniocladiinae.

Like the genera here included in the sub-family Hexagonellinae, *Goniocladia*, *Ramipora*, and the related genera and sub-genera described by Shulga-Nesterenko and Nikiforova from the Russian Carboniferous, appear to form a distinct group of genera, closely related phylogenetically to each other, within the Fistuliporidae, which should therefore be considered as a separate sub-family of the Fistuliporidae, the sub-family Goniocladiinae Waagen and Wentzel. This course is considered preferable to regarding both *Hexagonella* and the genera related to it, and *Goniocladia* and related genera, as belonging to two separate families both separated from the Fistuliporidae, as the characters in which each group differs from typical *Fistulipora* do not appear to be of sufficient importance for the formation of separate families, but to indicate closer phylogenetic relationship of groups of genera within the family.

Genus RAMIPORA Toula, 1875.

Ramipora Toula, 1875, 230; *Ramipora* Toula, Shulga-Nesterenko, 1933, 32, 54; Crockford, 1944, 192.

Sub-genus RAMIPORELLA Shulga-Nesterenko, 1933.

Ramiporella Shulga-Nesterenko, 1933, 39, 56.
Ramipora *with irregularly pinnate zoaria.*
Genotype: Ramipora (*Ramiporella*) *asimmetrica* Shulga-Nesterenko, 1933.
Range: Carboniferous.

Shulga-Nesterenko proposed that three sub-genera should be recognized within the genus *Ramipora* for forms which differ from typical *Ramipora* in having either irregularly pinnate or ramose zoaria, or zoaria with limited bifurcation, differing internally in the degree of development of vesicular tissue or in one case in the curvature of the zooecia. *Ramiporella*, the first of these three sub-genera, has a ramose or sub-pinnate zoarium which the species here described from Queensland resembles, and this species is therefore classified in this sub-genus.

RAMIPORA (RAMIPORELLA) FLEXUOSA, n. sp.   Pl. iii, figs. 4, 5; Text-fig. 21.

Holotype: F.5768B, Univ. Queensland Colln.

Horizon and locality: Riverleigh Limestone, Pors. 21 and 22, Par. Malmoe.

Fine, irregularly branching Ramipora; *zooecia in two to three rows on each side of the mesial lamina.*

The zoarium arises from a slightly spreading non-celluliferous base, from which two or three thin upright branches arise. The branches are bifoliate, and they typically divide in a plane at right angles to that of the mesial lamina, though one bifurcation in the same plane as the mesial lamina is shown; lateral branches are given off from the main stem at very irregular intervals, and at varying angles. The branches are thin, 0·4 to 0·75 mm. in width perpendicular to the mesial lamina, and about 0·5 to 1 mm. in thickness parallel to it; they are usually very much twisted. They are bifoliate, with the zooecia placed on each side of the mesial lamina, which runs from the centre of the reverse to the centre of the poriferous surface, forming a fine carina along the centre of each surface; the poriferous surface is sharply convex, the reverse rounded. Two to three rows of apertures occur on each side of the carina of the poriferous surface; there are usually three rows along each side of the main branch, but the arrangement of the apertures in these rows is not very regular. The central rows of apertures are not very strongly exserted, but the apertures in the rows closest to the reverse surface are frequently strongly exserted. The apertures are circular, 0·08 mm. in diameter, and no lunaria are shown; they are spaced usually with the centres of successive apertures in the same row from 0·33 to 0·65 mm. apart, and there are about 20 apertures in 10 mm. The surface between the apertures is solid; the reverse surface is finely granular, and is non-poriferous for a width of about 0·36 to 0·55 mm. on each side of its carina.

Owing to the silicification of the specimens, and their brittleness and very small size, it was not possible to prepare slides to show the internal structure; this is shown on broken surfaces of the branches to be very similar to that shown in described species of *Ramipora*: the zooecia are placed back to back along the mesial lamina for a

short distance, and then curve outwards rapidly to meet the surface almost at right angles; close to the mesial lamina a few small vesicles are developed between the zooecia, these being gradually replaced by dense tissue as the surface is approached.

From described species of *Ramipora* and of *Ramiporella* this species is distinguished by its extremely fine branches and by the irregular mode of branching of the zoarium.

<div align="center">Order TREPOSTOMATA.

Family BATOSTOMELLIDAE Ulrich.

Genus LEIOCLEMA Ulrich, 1882.</div>

Leioclema Ulrich, 1882, 14; *Leioclema* Ulrich, Ulrich, 1890, 376, 425; Nickles and Bassler (as *Lioclema*), 1900, 33, 302; Moore, 1929, 10; Duncan (as *Lioclema*), 1939, 248.

"*Zoarium ramose, lamellar, sub-globose or incrusting; surface frequently exhibiting distinct monticules or maculae; zooecia with sub-circular or irregularly petaloid apertures, separated by abundant angular mesopores, which in some species are open at the surface, in others closed; diaphragms few in the zooecia, abundant, sometimes crowded, in the mesopores; acanthopores numerous and strong in the typical species, small and inconspicuous in others.*" (Nickles and Bassler, 1900, 33.)

This genus has not previously been recorded from Australia but, as well as the species here described from the Lion Creek Limestone, the genus is known to occur in the Devonian of the Wellington district of New South Wales (specimen 7425, Sydney Univ. Colln.).

<div align="center">LEIOCLEMA POROSA, n. sp. Text-figs. 7, 8.</div>

Holotype: F.6856E, Australian Museum Colln.

Horizon and locality: Lion Creek Oolitic Limestone, Stanwell, near Rockhampton.

Leioclema with thin laminar zoaria; zooecia almost completely separated by a single row of angular mesopores; acanthopores not numerous.

The zoarium is a thin laminar expansion, reaching a maximum thickness of some 3 mm. and up to about 2 cm. in diameter. Small monticules in which the zooecial tubes are smaller and the mesopores larger and more numerous occur at distant intervals on the surface of the zoarium.

The zooecial tubes are sub-circular and slightly angular in outline; they are usually between 0·22 and 0·3 mm. in diameter. Small angular mesopores occur abundantly between the zooecia; a single row of these mesopores usually occurs between the zooecia, but occasionally the walls of adjacent zooecia are in contact for a short distance. In 7 sq. mm. there are about 50 zooecial tubes and about four times that number of mesopores. Because of the presence of numerous mesopores the walls of the zooecial tubes are not strongly thickened in the cortical zone. Small acanthopores occur rarely. In longitudinal sections the tubes are thin walled and recumbent for a short distance, about 0·3 mm., at the base of the colony, and then bend upwards to the surface. Thin complete diaphragms are abundant in the zooecial tubes, there being up to 8 in 1 mm. Tabulae are abundant in the mesopores, up to 12 occurring in 1 mm.

There is no described species of *Leioclema* with which this species could be closely compared.

<div align="center">Genus STENODISCUS Crockford, 1945.</div>

Stenodiscus Crockford, 1945, 21.

<div align="center">STENODISCUS STANWELLENSIS, n. sp. Text-figs. 9, 10.</div>

Stenopora leichardtii Nicholson and Etheridge, Etheridge, 1900, 9, Pl. i, figs. 10–12; [non] *Stenopora leichardtii* Nicholson and Etheridge, 1886, 179, Pl. iii, figs. 7–8.

Holotype: F.6857A, Australian Museum Colln.

Horizon and locality: Lion Creek Oolitic Limestone, Stanwell, near Rockhampton.

Small laminar, simulating massive, Stenodiscus; zooecial tube walls with small, distinct, close spaced monilae; acanthopores of two sizes numerous; thin complete diaphragms occasionally developed, mesopores very rare.

The zoaria of this species are small laminar colonies, up to about 7 mm. in their maximum height, and expanding over an area more than 20 mm. in diameter; each zoarium is made up of thin laminae 0·5 to 3 mm. in thickness, sometimes discontinuous or partly separated by sediment; the colonies in their thickest part simulate small massive zoaria, and their upper surfaces are irregular, this feature leading Etheridge to describe them as lobate masses.   Small indistinct monticules, about 1·5 mm. in diameter and composed of zooecia slightly larger than the average, are developed about 5 to 6 mm. apart on the surface.

The zooecia are tubular; they lie horizontal for about 1 mm. at the base of the colony and also at the base of each lamina, where a fresh layer of zooecia is developed above the thin epitheca occurring at the base of the lamina; above this they bend sharply upwards to meet the surface perpendicularly.   Moniliform thickenings appear in the walls of the tubes as soon as they bend upwards; the monilae are small, about 0·12 mm. in length and up to 0·65 mm. in their greatest thickness; about 8 monilae are developed in 1 mm.   The zooecial walls between the monilae and in the horizontal part of the zooecial tubes are extremely thin; in tangential section, therefore, the tube walls are either very thin, in which case the tubes themselves appear angular and polygonal, or else thickened, in which case the tubes are rounded, according to whether the section passes through the tube walls between, or at the level of, the monilae.   Where the tubes are thick walled, their diameter is usually 0·19 to 0·24 mm., their size being slightly larger, up to 0·27 mm. in diameter, in the monticules.   Acanthopores are numerous, and are of two sizes; of these the larger are less abundant, four or five occurring around each zooecial tube, and they are usually developed at an angle of the tube; the smaller acanthopores occur in a single row in the tube walls, and up to about 15 of these surround each tube.   Mesopores are of rare occurrence; they are found mainly in the monticules, where three or four occur in the area of each monticule.   Thin, complete diaphragms occur very occasionally in a few of the tubes.   In an area of 7 sq. mm. there are about 90 to 100 zooecial tubes, with about 4 to 6 mesopores in the same area.

Etheridge (1900) described and figured one of these specimens, which he referred to *Stenopora leichardtii* Nicholson and Etheridge, a species from the Permian of the Bowen River Coalfield in Queensland; these specimens, however, cannot be referred to *S. leichardtii*, from which they clearly differ in the arrangement and development of acanthopores, mesopores, monilae, etc.

This form is of especial interest since, although *Stenopora* is one of the most common and abundant genera in the Permian of Australia, no Carboniferous stenoporids, except this one form recorded by Etheridge, has hitherto been described from here. (De Koninck has made reference to the occurrence of *"Favosites ovata* Lonsdale" in the Lower Burindi Series at Glen William and Burragood in New South Wales; one of his figures (Pl. vii, fig. 5a) is probably a stenoporid but the description and figures leave some doubt about this, as Benson (1921, 23) has already discussed, and no other specimens of *Stenopora* are known to have been found in the Lower Carboniferous of New South Wales.)

In one of the thin sections of *Evactinopora irregularis*, however, a ramose batostomellid which appears to be a specimen of *Stenopora* s. str. is sectioned, but the preservation is too poor and the material insufficient for detailed description.

However, stenoporids (i.e., species of *Stenopora*, *Tabulipora* and *Stenodiscus*) have been described from the Carboniferous of the United States, the British Isles and Russia. This species from the Lion Creek Limestone does not closely resemble in the details of its structure any described form; it can readily be distinguished from any described species of stenoporid from the Permian of eastern Australia by the comparatively tiny size of its zooecial tubes, apart from any other differences.

Order CRYPTOSTOMATA Vine.
Family FENESTRELLINIDAE Bassler.
Genus FENESTRELLINA d'Orbigny, 1849.
Fenestrellina d'Orbigny, 1849, 501; *Fenestrellina* d'Orbigny, Bassler, 1935, 111.

FENESTRELLINA YARROLENSIS, n. sp. Pl. i, fig. 1; Text-fig. 16.

Holotype: F.5769C, Univ. Queensland Colln.

Horizon and locality: Oolitic Limestone, Por. 193, Par. Mundowran.

Very fine Fenestrellina; *fenestrules rectangular, one to two zooecia to a fenestrule; nodes high, sharp, closely and evenly spaced.*

The zoarium is very fine meshed, there being about 25 fenestrules and 30 branches in 10 mm. The branches are straight, 0·24 to 0·31 mm. wide, and bear two rows of zooecial apertures separated by a slight carina, on which there is a single row of high, spine-like nodes, placed 0·24 mm. apart; 42 of these nodes occur in 10 mm. Most of the zooecial apertures have been considerably enlarged by weathering, but where they are best preserved they are small and circular, 0·12 mm. in diameter, and are surrounded by slight peristomes. There are either one or two apertures to a fenestrule, and about 45 in 10 mm., the distance between the centres of successive apertures being 0·2 to 0·27 mm., but usually about 0·22 mm. The fenestrules are rectangular, 0·22 to 0·3 mm. long and 0·09 to 0·13 mm. wide; the width of the dissepiments is 0·06 to 0·13 mm., and the length of one fenestrule and one dissepiment from 0·35 to 0·4 mm. On the reverse surface both branches and dissepiments are evenly rounded, and they are of about the same thickness. Silicified fibrous tissue forms an overgrowth over part of the reverse surface.

A number of species similar in size to this form have been described from the Carboniferous of North America and Russia, but the spacing of the zooecia and of the nodes of this form is more distant compared with the size of the fenestrules than in any described species. *Fenestrellina pectinis* (Moore), 1929, from Pennsylvanian of Texas, is of similar size, but there are fewer fenestrules in 10 mm., and these are hour-glass shaped owing to the very regular arrangement of the apertures, two to a fenestrule; *F. limbata* (Foerste), 1887, is also similar in size, but has pyriform apertures, of which there are two to three to a fenestrule.

FENESTRELLINA, sp. indet. Text-figs. 17, 18.

Specimen: F.5768G, Univ. Queensland Colln.

Horizon and locality: Riverleigh Limestone, Pors. 21 and 22, Par. Malmoe.

Fenestrellina *with long, rectangular fenestrules and very thin branches and dissepiments; four to seven apertures to a fenestrule; carina absent.*

There are about 4 fenestrules and 10 branches in 10 mm. The branches are straight, 0·22 to 0·35 mm. wide, and bifurcate frequently. They are rounded on the obverse surface, and there are two rows of zooecial apertures, placed on the sides of the branches; no carina is developed, the surface between the apertures being ornamented only by swirling ridges and grooves; nodes are not well shown but appear to have been occasionally developed. The apertures are circular, 0·11 mm. in diameter, and they are surrounded by slight peristomes; there are usually four to seven, most often five to six, apertures to a fenestrule, the distance between the centres of successive apertures being 0·38 to 0·46 mm., and there are about 24 in 10 mm. The fenestrules are rectangular, about 1·3 to 2·0 mm. long and 0·5 to 0·75 mm. wide; the width of the dissepiments is 0·11 to 0·17 mm. On the reverse surface both branches and dissepiments are rounded and finely granular, the dissepiments being much thinner than the branches.

This very coarse *Fenestrellina*, with its distinctive slender branches without carinae, occurs associated with *Archimedes regina*, n. sp.

Genus POLYPORA M'Coy, 1845.

Polypora M'Coy, 1845, 207.

POLYPORA SULCIFERA, n. sp. Pl. i, fig. 2; Text-fig. 13.

Holotype: F.5768C, Univ. Queensland Colln.

Horizon and locality: Riverleigh Limestone, Pors. 21 and 22, Par. Malmoe.

Fine Polypora, *zooecia usually in 3 rows, 3 to 6 to a fenestrule; apertures strongly exserted, surface of branches deeply sulcate.*

The zoarium is fenestrate, with about 6 fenestrules and 11 branches in 10 mm. The branches are narrow and flattened, 0·35 to 0·4 mm. wide; usually there are 3 rows of zooecial apertures, with 3 to 5 before, and 2 to 3 after, bifurcation. The apertures are circular and are very small, 0·08 mm. in diameter; when perfectly preserved they are very much exserted and almost stalked. There are three to six zooecia to a fenestrule; over most of the colony there were probably five to six, as it is only where the branches were rapidly bifurcating and the fenestrules shortened, apparently close to the base of the colony, that there is a smaller number; the distance between the centres of successive apertures is 0·3 to 0·44 mm., and there are 29 apertures in 10 mm. The fenestrules are oval, from 0·86 to 1·96 mm. long and 0·2 to 0·27 mm. wide; the width of the dissepiments is 0·16 to 0·27 mm., and the length of one fenestrule and one dissepiment 1·1 to 2·2 mm. On the reverse surface both branches and dissepiments are granular; the dissepiments are usually about the same thickness as the branches, but are sometimes very much thinner.

The small dimensions of the zoarium, together with the strongly exserted apertures and deeply furrowed surface of the branches, distinguish this species from described species of *Polypora*. The occurrence of this species of *Polypora* in the Riverleigh Limestone is of interest because, amongst the comparatively large collections examined from the Burindi and Lower Kuttung Series in New South Wales, in which *Fenestrellina* and *Hemitrypa* are very abundant, there was not a single specimen of *Polypora*, and no specimens of this genus were observed in any of the other smaller collections from the Lower Carboniferous of Queensland.

<p style="text-align:center">Genus ARCHIMEDES Owen, 1842.</p>

Archimedes Owen, 1842, 19; *Archimedes* Hall, 1857, 176; *Archimedes* Hall, Condra and Elias, 1944, 1; synonym: *Archimedipora* d'Orbigny, 1850, 502; *Archimedipora* d'Orbigny, Easton, 1943, 142, and 1944, 406.

Growth-form consists of zoarial meshwork as in Fenestrellina, with branches bearing two rows of zooecial apertures on one side and connected by more or less regularly spaced cell-less dissepiments; coiled in a more or less regular helicoid, encrusted differentially by fibrous tissue; screw coiling sinuous or straight, slightly to heavily encrusted. (Adapted from Condra and Elias, 1944, 64.)

Genotype: Retepora archimedes Owen, 1842.

Range: Upper Silurian (?) to Permian.

The validity of this generic name has been the subject of lengthy discussion by Condra and Elias (1944) and by Easton (1943, 1944), and these writers have already discussed the history of the use of the names *Archimedes* and *Archimedipora* at some length. The present position with regard to these names is that Condra and Elias consider that *Archimedes* is the valid name for this group of fossils, and they regard Hall (1857) as its author, since they hold the view that Owen in 1842 designated the species "*Retepora Archimedes*" and not the genus *Archimedes*; they consider the genotype of *Archimedes* to be *Archimedes wortheni* Hall, 1857. Easton, on the other hand, holds that *Archimedipora* d'Orbigny, 1850, is the valid name for this genus of bryozoans, since d'Orbigny's publication antedates that of Hall, and there can be no possible doubt as to the identity of the genus to which the two names have been applied; d'Orbigny designated the species figured by Owen as "*Retepora Archimedes*" as genotype; as neotype of this species, Easton has selected the holotype of *Archimedes wortheni* Hall, 1857. Controversy has arisen as to the validity of this selection of a neotype, and it appears to me that, despite Easton's arguments to the contrary, Condra and Elias are correct in regarding this selection invalid because the holotype of *Archimedes wortheni* is not a topotype of Owen's species.

Even so, if Condra and Elias be correct in stating that Hall is the author of the name *Archimedes*, the fact still remains that *Archimedipora* was proposed for the same genus prior to Hall's publication in 1857.

Owen's original usage of the name *Archimedes* is incidental to a discussion of the age of the limestone in which it occurs, and his description of the specimen he figured

is ambiguous on the question of whether he intended to propose a new genus or a new
species; it appears to me that it is quite open to either interpretation, as Owen quite
clearly refers to both possibilities and refers to the form he figured as *Archimedes* in
the text and as *Retepora archimedes* in a foot-note. It therefore appears to me that
Owen (1842) can be considered the author of the generic name *Archimedes*, and there-
fore that *Archimedipora* d'Orbigny is a synonym; this course appears quite reasonable
from Owen's original discussion, and such an interpretation seems desirable in that
it avoids rejection of the long-used and well-known name *Archimedes* in favour of
Archimedipora; in this paper, therefore, *Archimedes* is used as the valid name for this
group of fossils. At the same time it is considered that, since so much controversy has
arisen about this name, and since the question of its validity is very involved and
ambiguous, and is undoubtedly open to varying interpretation by different authors,
application for a definite ruling upon this question should be made to the International
Commission on Zoological Nomenclature, when this Commission again commences to
function, in order to obtain stability in the naming of this genus.

Condra and Elias, in their monograph on this genus, have succeeded in the
enormous task of carefully and precisely revising and figuring almost all the described
species of the genus, and they have discussed every record of its occurrence. Apart
from one species, described from Spitzbergen by Toula in 1885, all of the described
species are from the United States and Russia, although single records of the occurrence
of the genus in Africa and in England, as well as Whitehouse's record of *Archimedes*
from Queensland, have been made.

Archimedes is extremely rare in the Silurian and Devonian, one species having
been described from each of these periods; it reaches its maximum abundance in the
Mississippian of the United States, 30 or more species being known from rocks of this
age; the majority of these species occurs in the Chester Series of Illinois. A smaller
number of species occurs in the Lower Pennsylvanian of Utah, but they are not known
in rocks of this age from any other part of the United States. In Russia, *Archimedes*
first appears in the Upper Carboniferous (doubtfully in the Middle Carboniferous)
and extends into the Lower Permian. It is therefore interesting that these two species
from Queensland have been found in rocks of Lower Carboniferous age; they are from
the Upper Viséan, and therefore from strata approximately equivalent in age to the
Chester Series in which the genus is so abundant in America. Condra and Elias
(1944, 184) state that:

"The Lower Pennsylvanian of Utah is the highest horizon in which *Archimedes*
is known in the United States. Since, in Northern Russia, the genus is only found
in the Middle Carboniferous and up, it is significant that with the advance of time
the *Archimedes* appears in stratigraphically higher rocks of the western than of the
eastern part of North America. Many other marine invertebrates, particularly
brachiopods of Pennsylvanian and Permian rocks of the western States, show marked
affinities with contemporaneous Himalayan and Uralian forms, which suggest the route
of migration between North America and Asia at the present time."

The early appearance of the genus in Australia, however, does not lend any support
to this theory, though it does not of necessity contradict it.

Condra and Elias have formulated the interesting hypothesis that *Archimedes* is a
symbiotic growth of a bryozoan and an alga. While the idea that the thick tissue of
the screw and flange may have been deposited by an alga as the meshwork was built
up by a species of *Fenestrellina* is extremely interesting, it is open to criticism on many
points, as Easton has indicated; many of the features which are explained by this
hypothesis can be equally well explained by comparison with the base of a normal
fenestellid colony, where excessive calcium carbonate is deposited to form a stronger
base, and rootlets, identical with those elaborately accounted for in this theory as
algal fibres, are very commonly developed as supports from the lower surface of a
fenestellid colony; examination of these deposits, the bryozoan origin of which is
beyond doubt, does not suggest that their origin could be different from the origin of
the axial support of *Archimedes* or the lateral supports developed in *Lyropora*. One

C

of the greatest weaknesses of Condra and Elias's presentation of this theory is that they have not attempted to compare in adequate detail the axial deposits of *Archimedes* with the deposits found strengthening the base of most large and old fenestellid colonies. Condra and Elias's explanation is so elaborately presented and has been based on such a vast amount of carefully prepared material that detailed criticism of it based on the silicified specimens from Queensland described in this paper would be inadequate, but further proof of their theory seems very necessary before it can be accepted.

ARCHIMEDES REGINA, n. sp.   Pl. ii, figs. 1, 2; Text-figs. 11, 20.

Archimedes (pars), Whitehouse, 1929, xii; Hill, 1934, 105.

Holotype: F.5768A = F.5608, Univ. Queensland Colln.

Horizon and locality: Riverleigh Limestone, Pors. 21 and 22, Par. Malmoe.

Archimedes *with a loosely-coiled cork-screw axis, with 1·5 volutions in 2 cm.; flange flaring; frond funnel-shaped, angle of divergence 60° to 70°, coarse meshed, with 10 branches and 6 to 7 fenestrules in 10 mm., 4 to 6 apertures to a fenestrule, carina with small, distant nodes.*

The holotype is portion of a screw, 3·5 cm. long, and comprising parts of four volutions, each with a considerable amount of the frond still attached. The rather thick shaft is cork-screw type; it is 4 mm. in diameter at this part of the zoarium, and it grades gradually into a flaring flange, about 13 to 16 mm. in diameter. On the expanse at the second volution preserved, the thickening of the flange is produced outwards along three or four branches and there is then a short gap in the expanse near the flange, as if part of the meshwork near the axis had been broken away during growth and the edges of the gap so formed had then been thickened. The volution height is about 1·3 cm., so that there are 1·5 volutions in 2 cm.

At the widest part preserved, the frond extends outwards for 3 cm. from the edge of the flange; it forms a funnel-shaped coil around the axis, from which it diverges at an angle of 60° to 70°. The frond is coarse meshed, there being 10 branches and 6 to 7 fenestrules in 10 mm. The branches are straight, about 0·5 mm. wide, and bear two rows of apertures; the carina is broad and indistinct, and there is a single row of small, rounded nodes, spaced 0·59 to 0·67 mm. apart. The apertures are small, circular (about 0·08 mm. in diameter), and are exserted; the distance between the centres of successive apertures is 0·28 to 0·36 mm., and there are about 31 apertures in 10 mm.; there are four to six apertures to a fenestrule. The fenestrules are oval, 0·95 to 1·68 mm. long and about 0·4 to 0·6 mm. wide; the dissepiments are without tubercles and are from 0·4 to 0·6 mm. wide. On the reverse surface both branches and dissepiments are evenly rounded, and they are of about the same thickness; the branches are ornamented on this surface by fine longitudinal striae. In addition, several pillars arise from the reverse surface and pass backwards perpendicularly to the surface of the frond beneath; these pillars range from about 0·75 to 2 mm. in diameter; rather numerous blunt nodules on the reverse surface of some parts of the frond represent the broken ends of additional pillars. The zooecia themselves are triangular in outline on the basal plate.

The upper end of the shaft appears to have been damaged during growth, and from the expanse on the left-hand side of the end (Pl. ii, fig. 1) and about 11 mm. from the axis a small adventitious shaft, of which only about 4 mm. near the base now remains, had commenced to grow.

This species occurs in the Riverleigh Limestone, which contains a *Lithostrotion-Amygdallophyllum* fauna, and is of Upper Viséan age, or possibly very slightly younger; the coral fauna has been described in detail and the age of the fauna fully discussed by Hill (1934; 1943, 62).

A. regina is remarkable amongst described species of *Archimedes* for the coarseness of the meshes of the frond, the largest known number of zooecia to a fenestrule in other species being from three to four. The most similar described species is *A. girtyi* (Condra and Elias), 1944, from the Pennnsylvanian of Utah, but this form, although it has a similar type of screw, has a very much finer mesh in the frond.

ARCHIMEDES SPIRALIS, n. sp. Pl. ii, figs. 3–6; Text-fig. 14.

Archimedes (pars), Whitehouse, 1929, xii; Hill, 1934, 105.

Holotype: F.5609, Univ. Queensland Colln.

Horizon and locality: Riverleigh Limestone, Pors. 21 and 22, Par. Malmoe.

Archimedes *with an exposed cylindrical screw and narrow, slightly flaring flange; 2·5 volutions to 2 cm.; angle of divergence of frond about 65° to 70°, frond coarse meshed.*

The holotype is portion of a long, curved screw, 10·3 cm. in its total length, and comprising about 13 volutions; the frond has been broken off along its line of junction with the axis. The screw was originally more or less fusiform, but was considerably deformed during the growth of the zoarium. Between the sixth and seventh volutions the shaft was fractured obliquely, and later more or less completely cemented together at this point; after fracture the lower part of the screw must have been more or less recumbent, and the upper part curved sharply upwards away from the original direction of growth; at the time the shaft was fractured the frond was broken away from the axis almost completely from the third to seventh volutions and partly from the eighth and ninth, and the tissue of the shaft and flange has almost completely grown over and covered the broken edges of the frond in this part of the zoarium; in addition, there was a profuse growth of rootlets, some of them very long, thick, and forked, from the lower side of the zoarium beneath and just above the fracture. Unfortunately the limestone in which this silicified specimen was preserved contains numerous tiny cross fractures, and these, crossing the fragile rootlets, caused them to break up into short segments as the specimen was gradually etched from its matrix; the broken bases of these rootlets remain on the shaft; one of the broken rootlets is shown in Pl. ii, fig. 3.

The shaft is cylindrical, being a "straight" mechanical screw, and is exposed and slightly fusiform; in the lowest two volutions preserved, the shaft is very thin and almost cork-screw in character; above this a ring of rootlets joins the shaft; these are up to 1·5 mm. thick where they join the shaft, and as they occur all around the shaft and not only on the lower side, supported the zoarium before it was fractured; the shaft then thickens abruptly and from this point on is cylindrical. The flange is narrow and slightly flaring, and leaves the shaft well exposed. The diameter of the shaft for the first two volutions was only about 1·7 mm.; above this the diameter of the shaft varies from 4·8 mm. at the base to 6·3 mm. at its thickest part and 4·3 mm. at the highest volution preserved; the maximum diameter of the flange is up to 9·0 mm. The volution height is 7·5 to 9·2 mm., so that there are almost 2·5 volutions in 2 cm.; the shaft is exposed for about 4 to 5 mm. between successive volutions, and the frond was given off at an angle of about 65° to 70°. The surface of the tissue of the shaft shows faint striae, which are straight on the exposed surface of the shaft and then flare outwards over the base and inwards over the upper surface of the flange.

Unfortunately the specimen fractured into small pieces so rapidly and the silicified tissue of the shaft and flange adhered so firmly to the surface of the branches of the fenestrate part of the zoarium, except where it had been naturally weathered along their contact, that it was impossible to expose the fenestrate part of the zoarium satisfactorily; the flange and part of the shaft at one volution were chipped off and the surface polished until the level of the meshwork was reached (Text-fig. 14). This shows that the fenestrules are very long, from at least more than 1·35 mm. to more than 1·6 mm. in length; from the broken edges of the frond also it is clear that the fenestrules must have been very long, as, although when the branches and dissepiments are weathered out from the shaft tissue they stand out very clearly and distinctly from the tissue of the flange, quite long distances of a branch are often shown clearly without any sign of a dissepiment being present or of its having been broken off. The width of the fenestrules is about 0·5 to 0·95 mm., and the width of the dissepiments 0·16 to 0·24 mm. The branches are about 0·21 mm. wide immediately after bifurcation, their width increasing to up to 0·4 mm.; there are two rows of

zooecia, increasing to three only immediately before a branch bifurcates; the zooecia are triangular in outline, and just after bifurcation they form an only slightly staggered row. There were evidently about six to seven zooecia to a fenestrule, and about 30 in 10 mm., the distance between the centres of successive apertures being 0·29 to 0·36 mm. The zooecial apertures are rounded, 0·11 mm. in diameter; no sign of a carina or of nodes could be seen. The dissepiments are depressed below the level of the branches on both obverse and reverse surfaces.

This species is differentiated from *A. regina*, n. sp., by its different type of screw and shorter volution height; the fenestrate part of the zoarium also appears to have had thinner branches, longer fenestrules, and finer branches than *A. regina*; these two species both occur in rocks of Upper Viséan age, associated with an *Amygdallophyllum-Lithostrotion* coral fauna. The coarseness of the fenestrate part of the zoarium separates this species from any other described species of *Archimedes*.

Family ACANTHOCLADIIDAE Zittel.
Genus PENNIRETEPORA d'Orbigny, 1849.

Penniretepora d'Orbigny, 1849, 501; *Penniretepora* d'Orbigny, Bassler, 1935, 165.

PENNIRETEPORA FRAGILIS, n. sp. Pl. iii, fig. 3; Text-fig. 19.

Holotype: F.5768D, Univ. Queensland Colln.
Horizon and locality: Riverleigh Limestone, Pors. 21 and 22, Par. Malmoe.

Fine Penniretepora; three, rarely two to five, zooecia between the origins of successive branches; slight carina, with small, distant nodes.

The zoarium is pinnate; the midrib is very thin, 0·5 mm. wide at its lower end, tapering gradually to 0·28 mm. at the top. The lateral branches, which are usually placed almost level with each other on opposite sides of the midrib, are given off at an angle of from 45° to 75°; they are from 0·25 to 0·4 mm. wide, and the carinae of successive branches are spaced 0·71 to 1·68 mm., but usually between 1·0 and 1·24 mm., apart; there are about 8·5 lateral branches in 10 mm. One of the lateral branches is itself pinnate, the first branch arising from it 1·03 mm. from the midrib; the spacing of the laterals on this branch is the same as their spacing on the midrib. The zooecial apertures are small and rounded, about 0·1 mm. in diameter, and they are in two rows, separated by a slight carina; small nodes were developed at distant intervals (about 0·9–1·2 mm.) on the carina. On the midrib there are usually three apertures between the points of origin of successive branches, but this number varies from two to five. There are 28 apertures in 10 mm. on the midrib, the distance between the centres of successive apertures being 0·31 to 0·44 mm.; the spacing is similar on the lateral branches. The surface between the apertures is ornamented by tiny granules, as is also the reverse surface.

Family RHABDOMESONTIDAE Vine.
Genus RHABDOMESON Young and Young, 1874.

Rhabdomeson Young and Young, 1874, 337; *Rhabdomeson* Young and Young, Moore, 1929, 141; Crockford, 1944, 166.

RHABDOMESON, sp. indet. Text-fig. 22.

Specimen: F.5769B, Univ. Queensland Colln.
Horizon and locality: Oolitic Limestone, Por. 193, Par. Mundowran.

The zoarium is ramose, the specimen being a hollow, cylindrical branch; the section is 2·16 mm. long, and passes through the centre of the zoarium; the zoarium is 1·19 mm. in width at the widest point cut in the section. The axial canal reaches a diameter of

Text-fig. 16.—*Fenestrellina yarrolensis*, n. sp., × 10. Obverse surface of the holotype.
Text-figs. 17–18.—*Fenestrellina*, sp. indet., × 10. Reverse and obverse surfaces of specimen F.5608, Queensland Univ. Colln.
Text-fig. 19.—*Penniretepora fragilis*, n. sp., × 10. Obverse surface of the holotype.
Text-fig. 21.—*Ramipora (Ramiporella) flexuosa*, n. sp., × 10. Two adjoining fragments of the holotype, which fractured along the broken surface shown.

0·36 mm., and appears to have been divided up by thin, straight diaphragms, spaced about 0·46 mm. apart. The zooecia are short, and they diverge from the outer margin of the axial canal at an angle of from about 30° to 45°, and on the lower right-hand side of the section, the only part in which the surface has not been worn away, they curve outwards at the base of the cortical zone to meet the surface at right angles. The zooecia are thin walled close to the axial tube, but the walls are about 0·08 mm. thick in the cortical zone, which is 0·28 to 0·32 mm. in radius. The apertures were about 0·16 mm. long and there were about 4 apertures in 1 mm. longitudinally. There are no diaphragms, but one or two very prominent superior hemisepta are developed in each zooecium at the base of the vestibule. A few comparatively large acanthopores are shown in section.

This single tiny specimen of *Rhabdomeson* was cut in one of the thin sections of the oolitic limestone containing *Evactinopora irregularis*, n. sp.; it is here figured and described as a record of the occurrence of this interesting genus in the Carboniferous of Queensland.
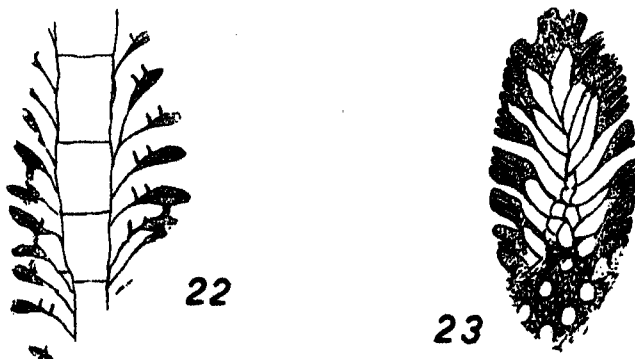
Text-fig. 22.—*Rhabdomeson*, sp. indet., × 20. Thin section through a zoarium cut in one of the slides of *Evactinopora irregularis* (specimen F.5769, Univ. Queensland Colln.).

Text-fig. 23.—*Streblotrypa*, sp. indet., × 20. Thin section through a zoarium cut in one of the slides of *Dybowskiella crescentica* (specimen 6448, Sydney Univ. Colln.).

Genus STREBLOTRYPA Ulrich, 1890.

Streblotrypa Ulrich, 1890, 403, 665; *Streblotrypa* Ulrich, Bassler, 1929, 66; Crockford, 1944, 168.

STREBLOTRYPA, sp. indet. Text-fig. 23.

Specimen: 6448B, Sydney Univ. Colln.

Horizon and locality: Crinoidal Limestone, Old Cannindah Homestead, near Monto, Queensland.

Two small fragments of a new species of *Streblotrypa* are shown in a section made from the crinoidal limestone at Cannindah, and they are described here for the purpose of recording the occurrence of this genus in the Lower Carboniferous of Queensland.

The zoarium is ramose, the branches being from 0·8 to 1 mm. in diameter; there appear to have been about 10 longitudinal rows of zooecial apertures. The apertures are oval, 0·13 × 0·16 mm. in diameter, and were arranged in regular longitudinal and apparently also in diagonal rows. The distance between the centres of successive apertures was about 0·31 mm. The area behind each aperture contains about five mesopore pits, and where they are most clearly shown these are arranged in quincunx. No acanthopores occur. The zooecial tubes are relatively rather long, being about 0·65 mm. in length. They diverge from an imaginary axis running through the centre of the branch and curve upwards for some distance, then bend outwards more sharply to the surface. Neither hemisepta nor diaphragms were observed in these sections. The mature zone is from about 0·16 to 0·22 mm. in width.

Like *Streblotrypa parallela*, n. sp., from the Lower Burindi Series of New South Wales, this species, with its zooecia diverging from the centre of the zoarium without the occurrence of a central bundle of small tubes, appears to be a typical Lower Carboniferous representative of this genus.

PART II. LOWER CARBONIFEROUS BRYOZOA FROM NEW SOUTH WALES.

Although Bryozoa are abundant in the lower Carboniferous rocks of New South Wales and were first recorded from them as long ago as 1847, when M'Coy (1847, 226) briefly recorded "*Fenestella undulata* Phil." and "*Glauconome* . . . allied to the *G. pluma* (Phil.)" from Dunvegan on the Paterson River, very little research has since been done on this group from the Carboniferous here. Benson (1921) has listed forms described or recorded from the Burindi Series of New South Wales prior to that date; the Bryozoa listed in his Index amount to a total of twenty-seven forms, referred at that time to fifteen genera. This list is deceptively long; it includes many records which, while they serve to indicate the localities at which Bryozoa principally occur, refer only to manuscript names, or to records, unaccompanied by a description or by figures, of the occurrence of either a species or a genus: and upon such records, which usually refer to one of the species described by Lonsdale from the Permian of Tasmania or to a European Carboniferous species, no reliance at all can be placed. Excluding these brief records, there were ten species occurring in the Burindi of New South Wales of which descriptions accompanied by figures had been given prior to the publication of Benson's Index. Of these ten species, three were species described as new by Chapman in 1920 (366-7), and the remainder, four European species and three new species, were described and figured by de Koninck in 1877 (128-140). Since 1921 no species occurring in the Lower Carboniferous of New South Wales has been described or figured, although the lists of fossils in several papers dealing with Carboniferous stratigraphy mention the occurrence of different genera and species of Bryozoa.

Fistulipora microscopica Chapman, *Cycloidotrypa australis* Chapman, and *Hallopora fruticosa* Chapman were described from material collected from the Burindi Series in the Parish of Moorowarra, near Somerton, *Cycloidotrypa* being described as a new genus. Unfortunately it is impossible to recognize these species from the descriptions or illustrations, and the type specimens (in the collections of the Mining Museum, Sydney, G. S. Reg. 4405, according to Benson) appear to be lost.

The specimens which de Koninck described were amongst the collections made in Australia by Rev. W. B. Clarke, and sent by him to Europe for description; when they were returned to Australia these specimens were placed in the Exhibition held in the Garden Palace in Sydney; this building was burnt in 1882 and the specimens therefore lost. The difficulty of identifying some of de Koninck's species is increased by the fact that several of the locality names which he used cannot now be traced and it is not therefore possible to collect topotype material.

The three new species which were described by de Koninck from Burindi localities are *Dendricopora hardyi*, *Fenestella propinqua*, and *Retepora ? laxa*, the first of these being the type of a new genus.

Dendricopora hardyi de Koninck (de Koninck attributes the specific name to Clarke, who had suggested it in manuscript) is a *Ptilopora*-like form; Bassler (1935, 90) has listed *Dendricopora* as a synonym of *Ptilopora* M'Coy, but according to de Koninck's description, *Dendricopora* possesses three instead of two rows of cells on both midrib and branches, and if this statement be correct, *Dendricopora* is a distinct genus. There were unfortunately no specimens in the collections used for this paper which could be identified with either de Koninck's figures or his description of this form; *Ptilopora konincki*, n. sp., has a similar growth form to *D. hardyi*, but has only two rows of zooecia, and is furthermore too small a species to be identified with de Koninck's description.

The other two new species described by de Koninck are revised in this paper as *Fenestrellina propinqua* (de Koninck) (pp. 35–36) and *Goniocladia laxa* (de Koninck) (pp. 29–31).

Four European species of Bryozoa were also described and figured by de Koninck from Burindi localities. These were recorded as *Penniretepora grandis, Fenestella plebeia, Fenestella multiporata* and *Polypora papillata,* all species originally described by M'Coy from the Carboniferous limestone of Ireland in 1845. The figures and descriptions of these four species given by de Koninck do not correspond sufficiently closely with those given by M'Coy to suggest that the Australian specimens were identical specifically with those described by M'Coy. *Fenestella fossula* Lonsdale, 1844, was considered by de Koninck to be a synonym of *Fenestella plebeia* M'Coy; Etheridge (1892) has already shown that de Koninck's description of specimens from the Burindi differs widely from Lonsdale's description of *F. fossula* from the Permian of Tasmania, and this record of the occurrence of *F. fossula* in the Burindi Series is therefore incorrect.

No species of bryozoan occurring in this material from the Burindi Series, or in material from marine intercalations in the Lower Kuttung Series in New South Wales, could be identified or even closely compared with any species known to occur in the Permian here. Indeed, the whole aspect of the two faunas is different; as has been pointed out in the introduction to this paper, the Carboniferous contains a fauna of a much more varied type than the Permian.

Amongst the fenestellids, the species occurring in the Burindi and Kuttung are of quite a different type to the Permian forms—in the Burindi and Lower Kuttung, fenestellids with small triangular or ovoid zooecia and fragile branches and dissepiments predominate, whilst the Permian forms are more robust, and almost without exception have larger, rhomboid zooecia. Benson (1921, 6) pointed out that of a total of some three hundred species known to occur in the Burindi, only thirteen species were at that time considered to extend into the Permian in New South Wales; of the thirteen species he so listed, five are Bryozoa, all of them fenestellids, and it is improbable that any of the species so listed do occur in both the Lower Carboniferous and Permian.

The full localities from which the specimens described from New South Wales were collected are as follows:

Glen William: Lower Burindi Series, Glen William, where the thin horizon in which Bryozoa occur abundantly forms a ridge west of the Glen William–Clarencetown Rd. in Pors. 201 and 204, west part of 22 and east part of 21, Par. Wallarobba, Co. Durham; this horizon lies about 200′ below the base of the Lower Kuttung Series in this area, and is believed to be the locality referred to as Glen William by de Koninck.

Hilldale: Lower Burindi Series, near Hilldale Railway Station, in Pors. 100 and 102, Par. Barford, Co. Durham; the horizon rich in Bryozoa lies about 400′ to 500′ below the base of the Lower Kuttung Series, and is probably to be correlated with the bryozoan horizon at Glen William.

Barrington: Outcrop of fossiliferous mudstones on the bank of the Williams R., about 100 yds. from Barrington House, Barrington Tops; this horizon probably lies within the Lower Burindi Series, but it cannot at present be closely correlated with horizons in other areas.

Rouchel Brook: Marine intercalation in the freshwater Lower Kuttung Series, banks of Rouchel Brook, just upstream from the Cameron Bridge, in Pors. 1 and 34, Par. Rouchel, Co. Durham; this horizon is a thin fossiliferous marine tuffaceous mudstone horizon intercalated in the Lower Kuttung Series about 800′ to 1,000′ above its base (a large part of the Lower Kuttung Series below this horizon consists of lava flows and coarse conglomerates). The facies and fauna of this horizon are distinct from those of the Upper Burindi limestone facies intercalated on higher horizons in the lower Kuttung Series.

Back Creek: Marine intercalation in the freshwater Lower Kuttung Series, in Back Creek at its junction with Woolooma Gully, in Por. 34, Par. Doon, Co. Durham,

This locality is close to Rouchel Brook (of which Back Creek is a tributary) and is believed to represent the same horizon.

Taree: Upper Burindi Series, in Taree Quarry, Por. 18, Par. Taree, Co. Macquarie; this area has been mapped and the fauna of this horizon has been discussed by Voisey (1938).

DESCRIPTION OF SPECIES.
Order CYCLOSTOMATA Busk.
Family FISTULIPORIDAE Ulrich.
Sub-family FISTULIPORINAE, n. sub-fam.
Genus FISTULIPORA M'Coy, 1850.

Fistulipora M'Coy, 1850, 131; *Fistulipora* M'Coy, Ulrich, 1890, 382, 474; Bassler, 1929, 41.

FISTULIPORA MIRARI, n. sp. Pl. iv, fig. 4; Text-fig. 26.

Holotype: 6432, Sydney Univ. Colln.

Horizon and locality: Lower Burindi Series, Glen William (holotype); Lower Burindi Series, Hilldale (7404, Sydney Univ. Colln.).

Fistulipora with a very thin, spreading unilaminate zoarium; zooecial tubes short, indented by slight lunaria, and separated by coarse vesicular tissue.

The zoarium is an extremely thin spreading expansion, 0·5 to 1 mm. in its total thickness, and may be either flat or rather buckled; none of the specimens observed were attached at the lower surface; the zoaria are unilaminate, the tubes arising from a very thin basal lamina and curving to meet the surface obliquely; the length of individual tubes is usually 0·8 to 1·1 mm. The zooecial apertures are 0·28 to 0·36 mm. in diameter, and they are indented by the development of a thin lunarium at the proximal side of each tube, the tube wall being curved to a slightly shorter radius around about one-third of its circumference (Text-fig. 26). In 7 sq. mm. there are about 18 to 23 zooecial apertures. The zooecia are separated by comparatively coarse vesicular tissue; there are one or two, rarely three, rows of vesicles between adjacent apertures, the vesicles ranging in diameter up to about 0·25 mm. At irregular and rather distant intervals the vesicles are aggregated to form spot-like maculae up to 2 mm. in diameter.

This species, which is readily recognized by its thin spreading unilaminate zoarium with maculae far less conspicuous than those of *Evactinopora trifoliata* and *Dichotrypa* ? *fragilis*, n. spp., is only one of several species of *Fistulipora* occurring in the Lower Burindi Series at Glen William and Hilldale; other species with distinct zooecial characters occur encrusting crinoid stems, etc., but are represented by specimens too poor for detailed description.

In the form of its zoarium this species closely resembles the genotype, *F. minor* M'Coy, 1850, from the Carboniferous of Derbyshire, but it differs in the details of its zooecial structure. *Fistulipora microscopica* Chapman, from the Burindi Series, Par. Moorowarra, near Somerton, had apparently a much thicker zoarium, and differed from this species in its much finer zooecial tubes and vesicular tissue.

Genus DYBOWSKIELLA Waagen and Wentzel, 1885.
DYBOWSKIELLA RHOMBOIDEA, n. sp. Text-fig. 32.

Holotype: 6426, Sydney Univ. Colln.

Horizon and locality: Upper Burindi Series, Taree Quarry in Por. 18, Par. Taree.

Laminar to small massive Dybowskiella; lunaria strong, their ends indenting and projecting into the zooecial tubes; zooecia tubular, with few diaphragms, and separated by coarse vesicular tissue, which is replaced by dense tissue as the surface is approached.

The zoaria are small irregularly shaped masses up to 1·5 cm. long, massive in appearance but actually built up of a number of laminae from 1 to 2 mm. or more in thickness; occasional laminae may extend some way beyond the edges of the main part of the colony. Small spot-like maculae about 1 × 1·5 mm. in diameter occur
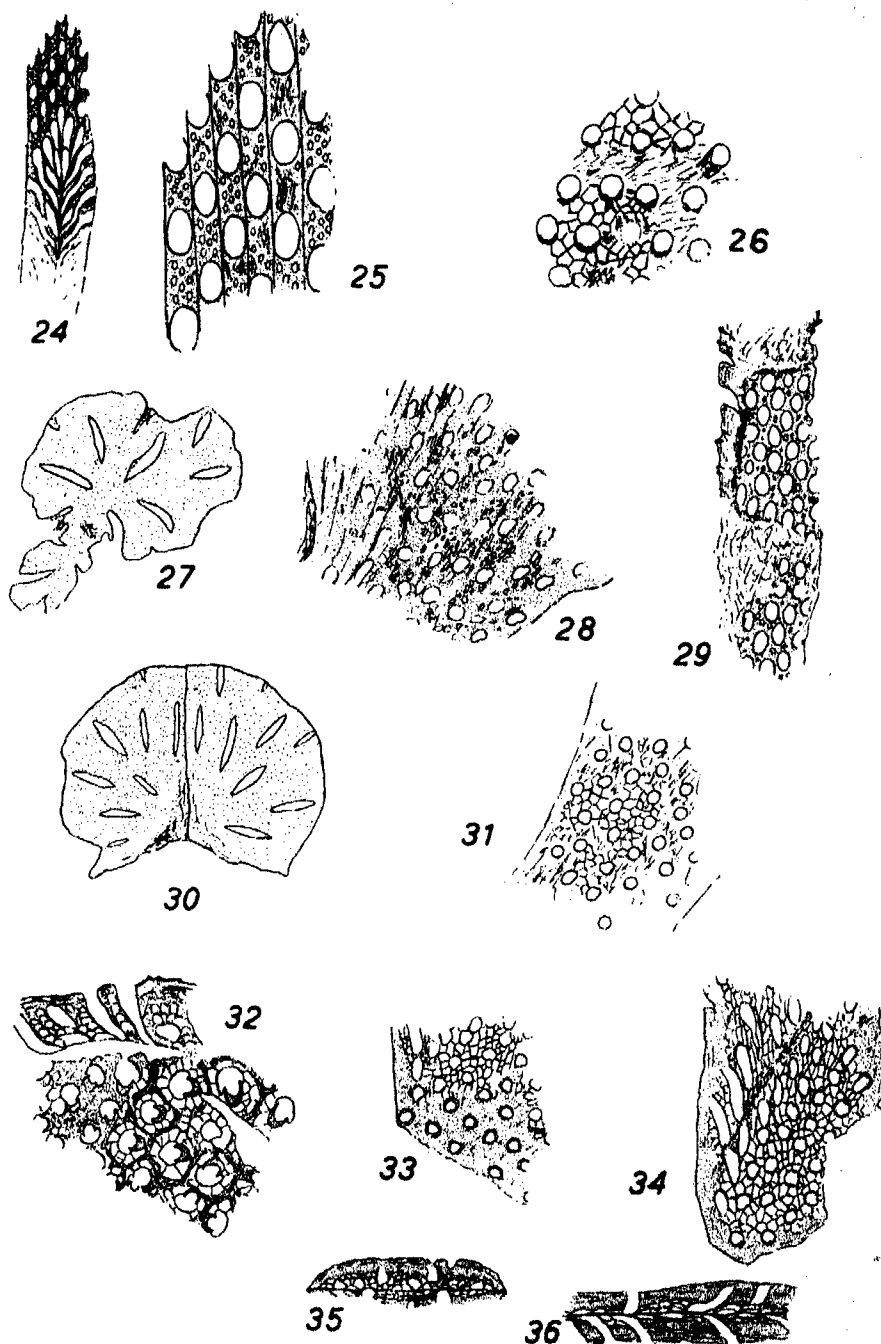
Text-figs. 24-25.—*Streblotrypa parallela*, n. sp. 24. Surface and oblique fractured surface of part of the holotype, × 10. 25. Surface of the holotype, × 30.

Text-fig. 26.—*Fistulipora mirari*. n. sp. Weathered surface of part of the holotype, × 10. The zooecial tubes stand out slightly above the weathered vesicles so that part of their outer surface is shown.

Text-figs. 27-28.—*Dichotrypa fragilis*, n. sp. 27. Outline diagram of the holotype, × 1. 28. Part of an oblique weathered surface of the holotype, passing from the level of the mesial

irregularly, these maculae being composed of vesicular tissue (or of solid tissue near the surface) and being surrounded by zooecial tubes larger than the average. In 7 sq. mm. there are about 23 zooecial apertures.

The zooecia are tubular; the lunaria are prominent and strongly developed, and they deeply indent the zooecial tubes, into which their ends project; the measurements of tubes of normal size are: a, 0·23 to 0·29 mm.; b, 0·28 to 0·35 mm. (usually more than 0·32 mm.); c, 0·11 to 0·14 mm.; d, 0·16 mm.; but zooecia of larger size are commonly found bordering the maculae. The lunaria occupy about one-third of the circumference of each tube and they are typically strongly thickened. An occasional thin complete diaphragm is developed in the zooecial tubes. The zooecia lie horizontal for a very short distance at the base of each lamina, and rapidly curve upwards to meet the surface almost at right angles. Comparatively coarse thin-walled vesicles separate the zooecia throughout the greater part of their length, and these vesicles are aggregated at intervals to form the maculae; two rows of these vesicles are found between adjacent zooecia, the line along which these two rows join being usually very distinct and thickened, giving a characteristic appearance to this form in tangential sections; it is to this apparent division of the zoarium into distinct rhombic areas that the specific name refers. As the surface is approached the vesicles are replaced by dense tissue, which occupies the spaces between the zooecia in the outer 0·25 to 0·8 mm. of each lamina.

The strong lunaria and the prominent thickening along the line of junction between the two rows of vesicles between adjacent zooecia readily distinguish this form from described species of the genus; it most closely resembles *D. crescentica*, n. sp., from Cannindah in Queensland, but differs in the slightly larger size of the zooecial tubes, the shape of the zooecia, and the structure of the vesicular tissue. Fragments of this species appear to be quite common in the limestone at the type locality, where it is associated with other fragmental Bryozoa (a species of *Fistulipora*, *Fistulamina* sp., etc.) in the matrix between and around the large compound coral *Aphrophyllum* cf. *hallense* Smith. The Taree limestone contains an Upper Viséan coral fauna.

Sub-family HEXAGONELLINAE, n. sub-fam.
Genus EVACTINOPORA Meek and Worthen, 1865.
EVACTINOPORA TRIFOLIATA, n. sp. Pl. iv, fig. 1; Text-figs. 30, 31.

Holotype: 6433, Sydney Univ. Colln.
Horizon and locality: Lower Burindi Series, Glen William.

Three-rayed Evactinopora; *rays very thin, bifoliate, surface with very elongate, depressed maculae; zooecia short, slightly indented by a thin lunarium, and separated by vesicular tissue.*

The zoarium is composed of three very thin vertical bifoliate rays, attached at their base to a *Spirifer*; the rays were placed at angles of approximately 150°, 110° and 100° to each other. The incomplete height of the rays at the centre of the zoarium is 2·2 cm.; their bases curve slightly downwards away from the centre along the *Spirifer*, and the maximum height shown is therefore greatest slightly away from the centre of the zoarium and is 2·7 cm.; the rays are up to 1·8 cm. wide at their widest point. Each ray is D-shaped in outline, and along their lower edges they are lightly attached to the *Spirifer* shell, and the bases of the rays appear to have spread very

lamina adjacent to a macula on the left-hand side to near the surface close to a macula on the right-hand side, × 10.
    Text-fig. 29.—"*Batostomella*" *lineata*, n. sp. Surface of the holotype, × 10.
    Text-figs. 30–31.—*Evactinopora trifoliata*, n. sp. 30. Outline diagram of two rays of the holotype, × 1. 31. Weathered surface of part of one ray adjoining two maculae, × 10.
    Text-fig. 32.—*Dybowskiella rhomboidea*, n. sp. Oblique section through the holotype, × 10.
    Text-figs. 33–36.—*Fistulamina inornata*, n. sp., × 10. 33. Oblique tangential section close to the surface of a topotype. 34. Oblique tangential section of a topotype passing from close to one surface at the lower end through to the mesial lamina and to the zooecia adjoining the mesial lamina on the other surface. 35. Transverse section of a topotype. 36. Vertical section of a topotype. (Slides in Sydney Univ. Colln.)

slightly over the surface of the shell; above this the rays are free. Long, slightly depressed maculae radiate from the base of the colony; these maculae are of strikingly large size, being from 5 to 10 mm. long and up to 2 mm. wide; they are also closely spaced, the distance between them being about 3 mm. longitudinally and 2·5 to 4 mm. transversely. These maculae apparently originally comprised a very thin layer of vesicular and solid tissue, now almost completely weathered away to leave a long oval space, but it is possible that they were originally spaces and, therefore, originally fenestrae rather than maculae.

The zooecial apertures are small and are slightly indented by a thin lunarium extending around about one-third of the circumference; the size of the zooecia is: *a,* 0·24–0·29 mm.; *b,* 0·2–0·27 mm.; *c,* 0·09–0·11 mm.; *d,* 0·14–0·16 mm. The zooecial tubes are very short indeed, being parallel to the mesial lamina for a short distance and then bending upwards to meet the surface rather obliquely. The interspaces between the zooecia are occupied by fine vesicles, one, rarely two, row of vesicles occurring between adjacent zooecia. The number of zooecia in 7 sq. mm. is 32 to 35.

This species appears to be an *Evactinopora* of very primitive type. The genus, which has hitherto been described only from the Burlington and Keokuk Groups of the Osage Series of the Mississippian of the United States, the Upper Viséan of Queensland and the Permian of Western Australia, comprises typically forms with four or more rays, which are free and typically have strong, comparatively thick rays, the surface being marked by small, solid maculae. This species possesses only three rays, these being extremely thin and fragile compared with those of other described species; however, although none of the species so far described has fewer than four rays, one undescribed species, occurring in the Permian of Western Australia, possesses only three very thin vertical rays, although in other ways it is a typical *Evactinopora.* This species also differs from other described species in being attached at its base (it is possible that *E. irregularis,* n. sp., may also have been an attached species); this indicates that it is a more primitive form than the free zoaria which developed later.

Genus FISTULAMINA, n. gen.

Genotype: *Fistulamina inornata,* n. sp.

Range: Carboniferous.

Zoarium bifoliate; branches ribbon-like, edges with narrow non-celluliferous margins; surface without maculae or hexagonellid ridges; internal structure fistuli-poroid, lunaria present; interzooecial spaces in the central part of the zoarium occupied by vesicular tissue, which is replaced by dense tissue as the surface is approached.

This genus is proposed to include forms which closely resemble *Sulcoretepora* externally but whose internal structure is similar to that found in *Hexagonella.* In *Sulcoretepora,* ribbon-like bifoliate zoaria with the zooecial apertures usually arranged in distinct longitudinal ranges, frequently separated by parallel ridges, are developed; lunaria and hemisepta are commonly present; internally, the zooecia are semi-cordate in outline, and are arranged in longitudinal rows between vertical double plates; vesicular tissue is developed between the zooecia near the mesial lamina, but closer to the surface the zooecia are separated by dense tissue. In *Fistulamina,* however, although the external appearance of the zoarium is similar, the zooecia are separated near the mesial lamina by vesicular tissue, without any development of vertical plates between the rows of zooecia; the zooecia themselves are tubular instead of semi-cordate, show no development of hemisepta, and possess poorly-developed lunaria; this type of internal structure is therefore closely related to *Hexagonella* and is quite different from that shown in *Sulcoretepora.* *Fistulamina* differs from *Hexagonella,* however, in lacking the characteristic hexagonellid ridges developed in that genus and particularly in its lack of maculae; maculae are strongly developed in the broad frond-like species and in some of the ribbon-like species of *Hexagonella,* and in the ribbon-like species the edges of the branches are usually not parallel but are lobed, with the non-celluliferous border of the branch continued inwards as a small macula

between the lobes; the zoaria of *Fistulamina* are also smaller and more flattened than those of *Hexagonella*.

Fistulamina inornata, n. sp., is a very common and characteristic form in the Lower Burindi and slightly younger rocks of New South Wales; a number of undescribed species congeneric with this form occur in the Burindi of New South Wales, in the Viséan at Mundubbera in Queensland, and also at Mt. Barney and other localities probably of Neerkol (Upper Carboniferous) age in Queensland. *Meekopora* ? *aperta* Ulrich, 1890 (p. 485), appears to be an American representative of this genus.

FISTULAMINA INORNATA, n. sp. Pl. iv, figs. 5–6; Text-figs. 33–36.

Holotype: 6431, Sydney Univ. Colln.

Horizon and locality: Lower Burindi Series, Glen William (holotype); Lower Burindi Series, Hilldale (7405, Sydney Univ. Colln.); marine intercalation near base of Lower Kuttung Series, Back Creek (7426, Sydney Univ. Colln.).

Zoaria narrow, bifoliate, ribbon-like; zooecial apertures small, with slight lunaria, arranged in 8 to 10 longitudinal rows and in diagonally intersecting rows on both sides of zoarium; zooecia tubular, separated by vesicular tissue near the mesial lamina, but by dense tissue as the surface is approached.

The zoarium consists of flattened bifoliate branches, 1·3 to 2·95 mm. wide, which bifurcate at fairly frequent intervals, generally between 0·6 and 1·5 cm.; bifurcation usually takes place in the plane of the mesial lamina. The branches are 0·5 to 0·7 mm. thick in the centre; both edges are rather blunt, the branches being elliptical in cross-section, and the non-poriferous margins of the branches are narrow and of about equal width on each side; a slight longitudinal ridge along each margin marks the position o the edges of the mesial lamina. The zooecial apertures are small and are rounded to very slightly oval; they are about 0·16 mm. in diameter. They are not indented by lunaria, and they are not surrounded by raised peristomes, although in thin sections slight lunaria can be distinguished. The apertures are usually arranged in 8 to 10 longitudinal rows on each surface, the number of rows being increased before bifurcation of the branches; they are also arranged in diagonally intersecting rows. There are about 19 apertures in each row in 10 mm., the distance between the centres of successive apertures being from 0·4 to 0·63 mm. The surface between the rows of apertures is smooth and finely granular; there are no longitudinal ridges between the rows of apertures.

The zooecia are short and tubular; they are placed back to back along the mesial lamina for a short distance and then bend outwards abruptly so that the vestibules meet the surface at right angles. In the central part of the zoarium near the mesial lamina the zooecia are separated by numerous small, thin-walled vesicles; close to the surface these are replaced by dense tissue. Neither hemisepta nor diaphragms are developed in the zooecial tubes.

Meekopora ? *aperta* Ulrich (1890, 485) shows a general resemblance to this species in its external appearance and internal structure, and should probably be referred to the same genus, though it is specifically distinct; *M.* ? *aperta* is from the Keokuk Group of Kentucky. Differences in size and in lunarial development readily distinguish *Fistulamina inornata* from *F. malmoensis* from the Viséan of Queensland. Species of *Sulcoretepora* which externally resemble this form are readily differentiated by differences in their internal structure.

Sub-family GONIOCLADIINAE Waagen and Pichl.

Genus GONIOCLADIA Etheridge, 1876.

Goniocladia Etheridge, 1876, 522; *Goniocladia* Etheridge, Bassler, 1929, 88; Moore, 1929, 154; Crockford, 1944, 157.

GONIOCLADIA LAXA de Koninck, 1878. Pl. v, figs. 3–5; Text-figs. 40, 41.

Retepora ? *laxa* de Koninck, 1878, 182, and 1892, 189; *Goniocladia laxa* de Koninck, Etheridge in Benson, 1921, 29.

Holotype: All of the specimens used by de Koninck were lost in a fire at the Garden Palace in Sydney in 1882; a neotype is not selected here as no topotype material is available.
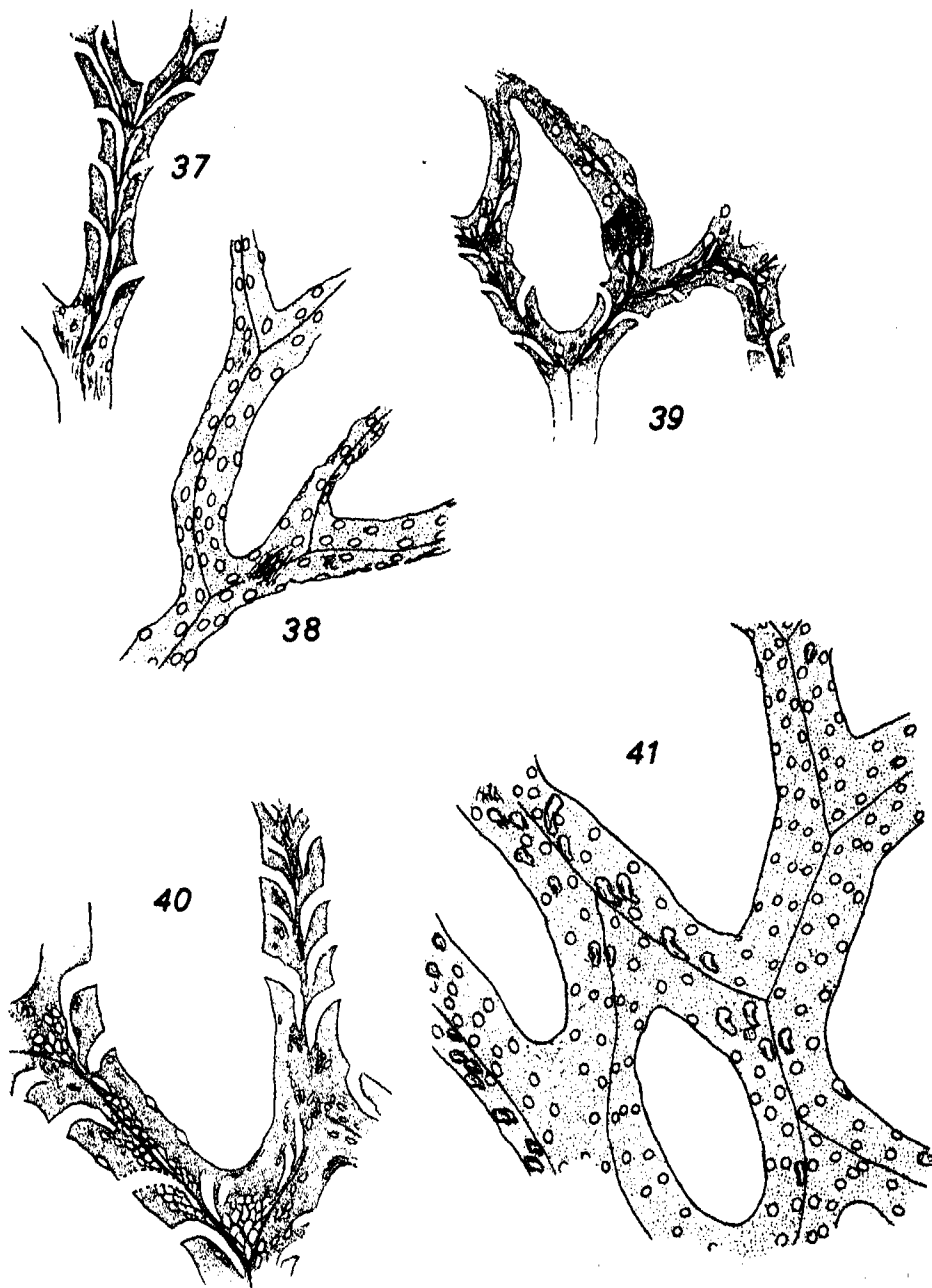
Text-figs. 37-38.—*Ramipora* (*Ramiporalia*) *bifurcata*, n. sp., x 10.   37. Fractured section through a branch of the holotype.   38. Cast of part of the obverse surface of the holotype.

Text-fig. 39.—*Goniocladia parva*, n. sp.   Fractured section through the holotype, x 10, the section being partly close to, and partly at, the obverse surface in the top central branch.

Text-figs. 40-41.—*Goniocladia laxa* (de Koninck), x 10.   40. Weathered section through part of a specimen from Hilldale (specimen figured on Pl. v, figs. 3, 4).   41. Cast of the obverse surface of a second specimen from Hilldale (specimen figured on Pl. v, fig. 5).

Horizon and locality: de Koninck's specimens were from "Colo Colo and Burragood", two Lower Burindi localities on the Allyn and Paterson Rivers. Benson (1913, 505) recorded but did not describe or figure this species, identified by Dun, from the Burindi Series at Crow Mountain, near Barraba. Etheridge, in an unpublished manuscript, states that he had specimens of this form from the Allyn River. The specimens which have been used for the revised description given here (specimens 5424, 5427 and 7411, Sydney Univ. Colln.) are from the Lower Burindi Series at Hilldale.

Coarse Goniocladia; *fenestrules large, irregularly polygonal; branches rather thin, sharply angular on the obverse and broadly rounded on the reverse surface, both surfaces being carinate; zooecial apertures in three, rarely more, rows on each side of the carina on the obverse surface; zooecia tubular, separated by fine vesicles close to the mesial lamina and by dense tissue closer to the surface.*

The zoarium is fenestrate; in spite of the large size of some of the specimens of this species—one incomplete specimen measured over 9 × 7 cm. and appears to be only a small part of a very large colony—none of the specimens used for this description show the form of the complete colony, which de Koninck stated was infundibuliform with the zooecial apertures placed on the outer surface of the branches. The zoarium forms a very coarse meshwork; the branches reticulate to form polygonal fenestrules of variable size; there are 1·5 to 2, rarely 2·5, fenestrules in 10 mm. longitudinally, and 2·5 to 4 fenestrules in the same distance transversely. The fenestrules vary in length from 2·0 to 8·3 mm., but are usually more than 4 mm. long; they are from 1 to 3·5 mm., generally between 2 and 3 mm., wide. The branches are from 0·63 to 1·5 mm., usually about 1·1 mm., wide. The non-celluliferous reverse surface of the branches, along the mid-line of which there is a fine ridge-like carina marking the position of the edges of the mesial lamina, is broad and smooth and only slightly convex; the obverse surface, however, is sharply carinate, and on each of its steeply sloping sides there are three, rarely four or five, rows of zooecial apertures. The apertures are round, about 0·22 mm. in diameter, and are surrounded by thin peristomes; these peristomes are most strongly developed on the row of apertures closest to the reverse surface, where they reach a height of up to 0·16 mm.

The mesial lamina runs from the centre of the reverse to the centre of the obverse surface; bifurcation of the branches takes place in a plane at right angles to that of the mesial lamina. The zooecia are tubular and are parallel to the mesial lamina for 0·75 to 1·0 mm., after which they bend outwards gradually to meet the surface obliquely. The zooecia are separated close to the mesial lamina by fine vesicular tissue, which is particularly strongly developed close to the reverse surface; the vesicles are replaced by dense tissue as the surface is approached, so that the interspaces are smooth and solid at the surface. Neither diaphragms nor hemisepta are developed.

This species is a smaller form than the genotype, *Goniocladia cellulifera* (Etheridge), from the Carboniferous of Scotland. *Goniocladia indica* Waagen and Pichl, 1885, from the Middle Productus Limestone of the Salt Ra., is of similar size to this species, but it differs in having broader branches, which are sharply carinate on the reverse and broadly rounded on the obverse surface, and in having very much coarser vesicular tissue, which apparently occupied a larger proportion of the interspaces than the vesicular tissue of *G. laxa*. *G. americana* Girty, 1908, from the Permian of Western Texas, has much stronger branches and differs in the appearance of the obverse and reverse surfaces. *G. grahamensis* Moore, 1929, from the Pennsylvanian of Texas, is a smaller species.

GONIOCLADIA PARVA, n. sp. Pl. v, fig. 2; Text-fig. 39.

Holotype: 8 on 7415, Sydney Univ. Colln.

Horizon and locality: Marine intercalation near the base of the Lower Kuttung Series, Rouchel Brook.

Fine Goniocladia; *fenestrules small, polygonal; branches thin, carinate on both obverse and reverse surfaces, the obverse surface being angular and the reverse rounded; zooecia in two rows on each side of the carina of the obverse surface; zooecia*

tubular, separated by fine vesicles near the mesial lamina, interapertural spaces solid at the surface.

The zoarium is fenestrate, with comparatively fine meshes; the branches are 0·5 to 0·7 mm., but usually about 0·56 mm., in width, and they are irregularly reticulated to form polygonal fenestrules of comparatively small size for the genus—2·7 to 3·1 mm. long × 1·0 to 1·5 mm. wide. There are about 3 fenestrules longitudinally and 4 to 6 horizontally in 10 mm. Each of the specimens of this species was broken through more or less completely at about the level of the centre of the branches, and although they showed the internal structure clearly, the external structure was not very well shown, and the fine tuffaceous mudstone matrix adheres so firmly to the surface that it was not possible to break the matrix away to show the external structure more clearly. The branches were sharply convex on the obverse and rather rounded on the reverse surface, both surfaces being carinate. Two rows of zooecial apertures occur on each side of the carina on the obverse surface; of these, the lower row is rather strongly exserted; several of the apertures are indented by lunaria, which occupy one-third of the circumference on the lower side of the aperture—these are particularly well developed in the lower row of zooecia. The apertures are about 0·14 mm. in diameter; the distance between the centres of successive apertures is 0·46 to 0·7, generally less than 0·6 mm., and there is an average of 19 apertures in 10 mm. The surface between the apertures and on the reverse surface is smooth.

Internally, the fine mesial lamina runs from the centre of the reverse to the centre of the obverse surface; the zooecial tubes run parallel to the mesial lamina for about two-thirds of their length, and then bend outwards rather gradually to the surface; the total length of each tube is about 0·63 to 0·7 mm. Close to the mesial lamina the tubes are separated by vesicular tissue, this being particularly strongly developed close to the reverse surface; as the surface is approached, this vesicular tissue is replaced by dense tissue. Neither diaphragms nor hemisepta are developed.

This species is a much finer form than *Goniocladia laxa* de Koninck, which occurs on a lower stratigraphical horizon. It is also a finer form than any species of this genus so far described from the Russian Carboniferous. *Goniocladia grahamensis* Moore, 1929, from the Pennsylvanian Upper Graham formation of Texas, has fenestrules of similar size (about 2·8 × 1·5 mm.); the branches of this species are comparatively broader, with zooecia typically in 3 (they range from 2 to 4) rows on each side of the carina; the zooecial apertures are spaced 0·3 to 0·72 mm. apart, averaging approximately 22 in 10 mm., according to measurements taken on Moore's figures of this species; the apertures are without lunaria, and his figures also show longer zooecia, the most complete zooecia shown in his figured thin sections being up to 0·7 mm. in length along the mesial lamina, while those in *G. parva* are only up to 0·7 mm. in their total length. The differences between these two forms, and particularly in the number of rows of zooecia and size of the zooecia, indicate that they should be referred to different species.

<div align="center">

Genus RAMIPORA Toula, 1875.

Sub-genus RAMIPORALIA Shulga-Nesterenko, 1933.

</div>

Ramiporalia Shulga-Nesterenko, 1933, 42, 59.

Genotype: *Ramipora (Ramiporalia) dichotoma* Shulga-Nesterenko, 1933.

Range: Carboniferous.

RAMIPORA (RAMIPORALIA) BIFURCATA, n. sp. Pl. v, fig. 1. Text-figs. 37, 38.

Holotype: 6429, Sydney Univ. Colln.

Horizon and locality: Lower Burindi Series, Glen William.

Ramiporalia *with regularly bifurcating bifoliate branches; branches carinate on both obverse and reverse surfaces, the obverse surface being angular and the reverse rounded; zooecial apertures in 3, less often 2, rows on each side of carina of obverse surface; zooecia separated by fine vesicular tissue close to the mesial lamina, interapertural spaces solid at the surface.*

The zoarium is composed of narrow bifoliate branches, 0·55 to 0·83 mm. in width and about 0·8 mm. in thickness along the mesial lamina; these branches bifurcate in a plane at right angles to the mesial lamina at frequent and regular intervals, usually between 2·7 and 3·5 mm. There is no sign of any anastomosis of branches of the colony. The mesial lamina, which runs from the centre of the obverse to the centre of the reverse surface, projects sharply above each surface to form a sharp ridge-like carina. Three, sometimes two, rows of zooecial apertures occur on each side of the carina of the obverse surface, which is more sharply convex than the reverse; the apertures are rounded to slightly oval, 0·17 to 0·22 mm. in diameter, the largest apertures occurring in the row of zooecia closest to the reverse surface; each aperture is surrounded by a thin, relatively high peristome. In 10 mm. there are about 18 apertures in each row, the distance between the centres of successive apertures being between 0·44 and 0·62 mm. The reverse surface is broadly rounded and is non-celluliferous; it appears to have been very coarsely granular. Internally, the zooecia lie parallel to the mesial lamina for about 0·7 mm., then they bend outwards to the surface. Close to the mesial lamina the zooecia are separated by numerous small vesicles, which are especially strongly developed close to the reverse surface; these vesicles are replaced by dense tissue as the surface is approached.

The mode of growth of this species and the greater number of rows of apertures distinguish it from *Goniocladia parva*, n. sp., which occurs in the overlying Lower Kuttung Series. An undescribed phylloporinid occurs associated with this species, but is distinguished by the fact that its branches, although regularly bifurcating, are unilaminar and not bifoliate, and that they are without carinae on either the obverse or reverse surfaces; the material of this phylloporinid is too poor for detailed description. From *Ramipora* (*Ramiporalia*) *dichotoma* Shulga-Nesterenko, 1933, which has a similar growth form, this Burindi species is readily distinguished by its different measurements.

Material from this and other localities in the Lower Carboniferous of New South Wales very frequently contains fragmentary specimens of species of *Ramipora*, too poorly preserved for detailed description.

Order TREPOSTOMATA Ulrich.
Family BATOSTOMELLIDAE Ulrich.
Genus BATOSTOMELLA Ulrich, 1882.

Batostomella (pars), Ulrich, 1882, 141, 154; *Batostomella* (pars), Ulrich, Ulrich, 1890, 375, 432; *Batostomella* Ulrich, Bassler, 1929, 60.

"*Zoarium ramose, branches slender; zooecia with few diaphragms; apertures of zooecia small, circular or oval; interspaces rounded or canaliculate, spinulose, the acanthopores small and usually very numerous; mesopores small, with sub-circular openings.*" (Nickles and Bassler, 1900, 32.)

Genotype: *Batostomella gracilis* (Nicholson), 1874.

Range: Ordovician (?) to Permian.

The validity of this generic name is doubtful. In his original description of this genus, Ulrich included four species and one variety (listed by him under the names of *Chaetetes granuliferus* Ulrich, *C. gracilis* James, *Trematopora annulifera* Whitfield, and *M.* (*Calamopora*) *tumida* Phillips, and var. *miliaria* Nicholson) and also stated that three undescribed species, of which he knew, should be referred here. Of the described species, the first three were from the Ordovician and the others from the Carboniferous; Ulrich did not name any one of these species as genotype in his original description (1882, 154) or discussion (1882, 141) of this genus. In 1890 Ulrich again published a diagnosis of this genus; in this he states that the "types" are "*B. spinulosa* n. sp. and *B. gracilis* Nicholson"; *B. gracilis* Nicholson is *Chaetetes gracilis* James of Ulrich's earlier list of species belonging to this genus, the name having been first used by James in manuscript and later published by Nicholson. Later authors have almost universally quoted *Batostomella spinulosa* as the genotype of *Batostomella*, but since this is not one of the species originally referred to the genus by Ulrich (unfortunately

Ulrich does not state in his description in 1890 whether *B. spinulosa* was one of the "undescribed species" he earlier referred to *Batostomella* or not) this course is inadmissible. The genotype is therefore *Chaetetes gracilis* Nicholson, which has long been removed from *Batostomella* and placed in *Bythopora* Miller and Dyer, 1878; if this classification of *Chaetetes gracilis* be correct (I have not access to any description of the genotype of *Bythopora* for comparison), *Batostomella* must be considered a synonym of *Bythopora*.

According to Bassler (1934, 54) two other generic names are available to replace *Batostomella*; these are *Geinitzella* Waagen and Wentzel, 1886, and *Batostomellina* Vinassa de Regny, 1920.

The status of *Geinitzella* is extremely involved; Waagen and Wentzel referred two species to the genus, as *Geinitzella columnaris* (Schlotheim) and *G. crassa* (Lonsdale); in their lengthy synonymy of *G. columnaris* they included as synonyms a large number of earlier described species, and in their description they recognize four varieties of this species; of these, Lee (1912, 152) has selected the variety they figured as *Geinitzella columnaris* var. *incrustans* (Geinitz) as genotype. While most of the figures of *Geinitzella* given by Waagen and Wentzel have been regarded as showing that his genus is a synonym of *Batostomella*, this does not apply, as Bassler (1929) has already pointed out, to *G. columnaris* var. *incrustans*; this particular variety, of which only two longitudinal sections are figured, should apparently be referred either to *Dyscritella* or *Stenopora*—no diaphragms are shown in any of the tubes cut in the figured sections, and in places the walls are irregularly thickened so as to suggest slight beading, so that this species is probably a *Stenopora*. Hence, since Lee's designation of *Geinitzella columnaris* var. *incrustans* as genotype must be accepted, the generic name *Geinitzella* is not available to replace *Batostomella*.

The second synonym of *Batostomella* listed by Bassler is *Batostomellina* Vinassa de Regny, 1920. The genotype of this genus is *Trematopora granulifera* Hall, 1852, from the Rochester Shale of New York; this species has been revised by Bassler (1906, 28). The original diagnosis of this genus by Vinassa de Regny is "*Batostomella tabulis nullis*"; the type species certainly is without tabulae, and therefore substitution of the name *Batostomellina* for *Batostomella* is not possible; *Batostomellina* may be a synonym of *Dyscritella*, but this is not certain, since revision of many batostomellids has revealed significant differences in wall structures, etc., between earlier and later Palaeozoic forms (Duncan, 1936).

A new name is therefore necessary for this genus of bryozoans, and consequently also for the family Batostomellidae, unless application is made for suspension of the *Rules of Nomenclature*. This procedure is best left until it can be based upon a comprehensive revision of the genera whose status is involved in this question.

"BATOSTOMELLA" LINEATA, n. sp.   Text-fig. 29.

Holotype: F.42112D, Australian Museum Colln.

Horizon and locality: Burindi Series, near Barrington House, Williams River, Barrington Tops.

Fine "Batostomella"; acanthopores small, numerous; mesopores developed at the angles of the apertures; zooecial apertures oval and comparatively large.

The zoarium is ramose; the branches are cylindrical, 1·18 to 1·36 mm. in width; no maculae appear to have been developed. The apertures are oval to almost round, from 0·19 to 0·24 mm. × 0·13 to 0·19 mm. in diameter; they are arranged in irregular diagonal rows. In 1 mm. longitudinally there are about 3 zooecial apertures; the interspaces between the apertures are rounded and bear numerous tiny, blunt, spine-like acanthopores, which are usually almost worn off so that only their bases remain, but which when they are well preserved may project up to 0·02 mm. above the surface of the zoarium; these acanthopores appear to have all been of the same size. Small rounded to oval mesopores, up to about 0·1 mm. in diameter, occur usually at each angle of the apertures, so that about five occur around each aperture. The interspaces

between the zooecia are from 0·05 to 0·1 mm. wide transversely and up to 0·22 mm. thick longitudinally.

The cortical zone occupies about one-fifth to one-quarter of the radius of the zoarium, its width being 0·24 to 0·32 mm. The zooecia are tubular, and bend from the axial zone (where they are very thin walled) to the cortical zone at an angle of about 60°; the walls are abruptly thickened in the cortical zone, giving the broad solid interspaces shown at the surface. A single thin complete diaphragm occurs in some tubes just within the bend in the zooecial tubes.

This species is a typical member of the group of forms congeneric with *B. spinulosa* (Ulrich).

<div align="center">

Order CRYPTOSTOMATA Vine.

Family FENESTRELLINIDAE Bassler.

Genus FENESTRELLINA d'Orbigny, 1849.

</div>

Fenestrellina d'Orbigny, 1849, 501; *Fenestrellina* d'Orbigny, Bassler, 1935, 111. Homonym: *Fenestella* Lonsdale, 1839.

<div align="center">

FENESTRELLINA PROPINQUA (de Koninck), 1877. Pl. vi, fig. 4; Text-fig. 50.

</div>

Fenestella propinqua de Koninck, 1877, 174, Pl. viii, fig. 3 (1898, 133, Pl. viii, fig. 3); *Fenestella propinqua* de Koninck, Benson, 1921, 27; [non] *F. ampla* ? Dana (a Permian form referred to this species by de Koninck).

Neotype: 2403, Sydney Univ. Colln. (de Koninck's type specimens formed part of the collections made by Rev. W. B. Clarke; on being returned to Australia, these specimens were exhibited in the Garden Palace, which was burnt in 1882.)

Horizon and locality: Lower Burindi Series, Glen William (original locality of de Koninck's specimens and locality of neotype chosen here); Lower Burindi Series, Hilldale (specimens 7401, 7406, 7412, Sydney Univ. Colln.); marine intercalation near base of Lower Kuttung Series, Back Creek (specimen 7426, Sydney Univ. Colln.); Burindi Series, Barrington House, Williams R., Barrington Tops (F.42112F, Australian Museum Colln.).

Coarse Fenestrellina; *branches thin, fenestrules large and irregularly rectangular; zooecia in two rows, with usually 6 to 7 zooecia to a fenestrule; slight carina with a single row of very small nodes.*

The zoarium is fenestrate; de Koninck states that the colony was funnel-shaped and implies that the inner surface was celluliferous. There are 10 to 11 branches and 4 to 5 fenestrules in 10 mm. The branches are thin, 0·21 to 0·35 mm. wide, and are fairly straight; in some parts of a specimen they may branch within 2 or 3 fenestrules, but at times the bifurcations may become very distant. There are two rows of small round zooecial apertures, 0·08 mm. in diameter, and surrounded by thin, distinct peristomes; increase to three rows of apertures occurs only immediately before bifurcation; the two rows of apertures are separated by a very faint carina, which bears a single row of very small nodes; the spacing of these nodes is unfortunately not well shown, but appears to have been about 0·42 mm. apart. There are usually 6 or 7 apertures to a fenestrule, the number ranging from 5½ to 10, with occasionally abnormally short or long fenestrules with fewer or more zooecia; the distance between the centres of successive apertures is between 0·27 and 0·36 mm., and there are about 32 apertures in 10 mm. The fenestrules are irregularly rectangular in outline; they are generally from 1·5 to 2·7 mm. long, but a few fenestrules may be abnormally short or long. The dissepiments are 0·06 to 0·4 mm. wide. The dissepiments are depressed below the level of the branches on the obverse surface, and on this surface they bear a strong carina; on the reverse they are of about the same thickness as the branches, and both are smooth and evenly rounded. The zooecia are ovoid in shape.

The neotype and other specimens used in this description compare closely with de Koninck's original description and figures of specimens from Glen William; this form has a very characteristic appearance (Pl. vi, fig. 4), and is a common and easily identified form in the Burindi of New South Wales. De Koninck considered this form

the same as a species figured by Dana in 1849 from the Permian at Glendon as
"*Fenestella ampla* ?"; Dana's species is quite unrecognizable from his figures and brief
description, and it is unlikely that the species he figured was *F. propinqua*. *F. propinqua*
has also been recorded without descriptions or figures by a number of more recent
workers from localities in the Upper Marine Series of the Hunter River district and the
Macleay Series of the Macleay River district of New South Wales and also from the
Lyons Series of the North-West Basin in Western Australia (see Raggatt and Fletcher,
1937, 172); it is most improbable that any of these records refer to the occurrence of
de Koninck's species.

In one or two of the specimens used for this description there is a tendency for
one of the branches to bifurcate more rapidly than the others and so to give a slightly
pinnate appearance to part of the zoarium; this pinnate appearance slightly developed
is common in several of the Burindi fenestellids, and one species of this type was
recorded as "*Fenestella gracilis* ? J. D. Dana" by de Koninck from Burragood, a
Burindi locality on the Paterson River; it is not possible to recognize this species
from de Koninck's description (the specimens are not figured). *F. gracilis* Dana, 1849,
is from a Permian locality, and is also unrecognizable. *Ptilopora* and *Penniretepora*
occur quite commonly in the Lower Burindi and Lower Kuttung Series, and it is
therefore interesting to find this slight tendency towards pinnate growth in some of
the associated fenestellids.

FENESTRELLINA ACABINATA, n. sp.   Pl. vi, fig. 3; Text-fig. 45.

Holotype: 7402, Sydney Univ. Colln.

Horizon and locality: Lower Burindi Series, Hilldale (holotype); Lower Burindi
Series, Glen William (specimen 6438, Sydney Univ. Colln.).

Fine Fenestrellina; *branches straight to slightly sinuous, carina and nodes absent;*
zooecial apertures strongly exserted, in two rows, 3 to 4 zooecia to a fenestrule.

The zoarium is infundibuliform, the internal surface being celluliferous; in 10 mm.
there are 10 to 11, rarely 13, fenestrules, and 19 to 24 branches. The branches are
straight, 0·21 to 0·32 mm. wide; the zooecial apertures are in two rows, and no carina
is shown, the centre of the branches on the obverse surface being slightly depressed
and ornamented by a few faint discontinuous longitudinal striae; no nodes are
developed. The apertures are small and round, 0·08 mm. in diameter, and they are
very strongly exserted, being almost stalked in appearance; there are 3 to 4 apertures
to a fenestrule, and about 40 in 10 mm., the distance between the centres of successive
apertures being 0·22 to 0·32 mm. The fenestrules are oval, 0·55 to 0·87 mm. (generally
between 0·68 and 0·82 mm.) long and 0·2 to 0·4 mm. wide; the width of the dissepiments
is 0·1 to 0·21 mm., and the length of one fenestrule and one dissepiment 0·71 to 1·0 mm.
The zooecial cells are ovoid in outline; where the specimens have been slightly
weathered their shape is well shown in casts, and marked inferior hemisepta are
developed in the zooecia; on the surface of the branches, and placed adjacent to the
apertures, swollen surface cells the same as those occurring in some of the Permian
Fenestellidae in New South Wales are occasionally developed. On the obverse surface
the dissepiments are rounded and are placed at the same level as the branches, but
they are depressed below the level of the branches on the reverse surface; the backs
of the cells are covered on the reverse surface by only a very thin layer of calcium
carbonate, showing longitudinal striae close to the backs of the cells and being finely
granular at the surface.

This fine species is somewhat similar in size to the associated *Hemitrypa clarkei*,
n. sp., but an examination of the details of their appearance readily serves to distinguish
these two species from each other.

FENESTRELLINA CRIBRIFORMIS, n. sp.   Text-fig. 46.

Holotype: 7415A, Sydney Univ. Colln.

Horizon and locality: Marine intercalation near the base of the Lower Kuttung
Series, Rouchel Brook.

Fenestrellina with very thin branches; 3 to 5 zooecia to a fenestrule.

There are 8 to 11 fenestrules and 18 to 21 branches in 10 mm. The branches are very thin, 0·19 to 0·3 mm. wide, and are straight, branching at only very distant intervals; they bear two rows of small zooecial apertures, placed on either side of a slight median carina; on this carina small nodes are developed at distant intervals, but these are readily worn away and unfortunately are not well shown in any of the specimens examined. The apertures, which are strongly exserted, are round and 0·09 mm. in diameter; there are 3 to 5 apertures to a fenestrule and about 36 in 10 mm., the distance between the centres of successive apertures being 0·22 to 0·34 mm.; increase to three rows of zooecia occurs only immediately before bifurcation. The fenestrules are rectangular in outline, 0·71 to 1·28 mm. long and about 0·2 to 0·55 mm. wide; the dissepiments are 0·06 to 0·13 mm. wide and are very much thinner than the branches. The zooecia are ovoid to rhomboidal in shape. The reverse surface of the branches is smooth and evenly rounded.

This species is a larger form and is distinguished by the spacing of its zooecial apertures and by the appearance of the obverse surface from *Hemitrypa clarkei* and *Fenestrellina acarinata*, which occur on a lower stratigraphical horizon.

FENESTRELLINA ROUCHELI, n. sp. Text-fig. 49.

Holotype: 7414 and 7415B (reverse), Sydney Univ. Colln.

Horizon and locality: Marine intercalation near the base of the Lower Kuttung Series, Rouchel Brook.

Fenestrellina *with 4 to 7 zooecia to a fenestrule; carina slight, nodes not developed.*

The zoarium is fenestrate; in 10 mm. there are 13 to 17 branches and 5 to 7 fenestrules. The branches are comparatively broad, 0·24 to 0·36 mm. in width, and they bear two rows of zooecial apertures, placed on either side of a very slight carina; no nodes appear to be developed. Bifurcation of the branches occurs at infrequent intervals, and increase to three rows of zooecia occurs only immediately before bifurcation. The apertures are round, 0·09 mm. in diameter, and they are not very strongly exserted; there are 4 to 7 apertures to a fenestrule, and 33 in 10 mm., the distance between the centres of successive apertures being 0·24 to 0·38 mm. The fenestrules are oval to almost rectangular in outline, and are from 1·0 to 2·25 mm. long and 0·2 to 0·6 mm. wide; the width of the dissepiments is 0·11 to 0·32 mm., and the total length of one fenestrule and one dissepiment is 1·1 to 2·37 mm. The reverse surface of both branches and dissepiments is smooth and evenly rounded, the branches being considerably thicker than the dissepiments.

The finer zoarium, with a smaller number of zooecia to a fenestrule, and the relatively thicker branches, distinguish this species from *F. propinqua* (de Koninck).

FENESTRELLINA BARRINGTONENSIS, n. sp. Text-figs. 42, 43.

Holotype: F.42112G, Australian Museum Colln.

Horizon and locality: Burindi Series, near Barrington House, Williams River, Barrington Tops.

Very fine Fenestrellina; *two zooecia to a fenestrule; slight carina with small, sharp, closely-spaced nodes.*

The zoarium is fenestrate and is very fine meshed, there being about 22 fenestrules and 30 to 32 branches in 10 mm. The branches are straight and are very thin, 0·15 to 0·19 mm. in width; they bifurcate comparatively frequently, often within four or five fenestrules. There are two rows of zooecial apertures, increasing to three only immediately before bifurcation; a slight ridge-like median carina is developed, and this bears a single row of small sharp nodes, spaced 0·16 to 0·25 mm. apart, with about 50 in 10 mm. The zooecial apertures are extremely small, being only about 0·05 mm. in diameter; they are surrounded by slight but distinct peristomes. There are two apertures to a fenestrule, these being so placed that one occurs at the end of each dissepiment and the other at the centre of each fenestrule; the distance between the centres of successive apertures is 0·19 to 0·24 mm., and there are about 46 apertures in 10 mm. The fenestrules are oval, 0·28 to 0·48 mm. long and 0·12 to 0·19 mm. wide;

the width of the dissepiments is from 0·03 to 0·08 mm., and the total length of one fenestrule and one dissepiment is from 0·42 to 0·52 mm.

FENESTRELLINA CELLULOSA, n. sp.   Text-fig. 44.

Holotype: F.42113H, Australian Museum Colln.

Horizon and locality: Burindi Series, Barrington House, Williams River, Barrington Tops.

Fine Fenestrellina, *with three to four zooecia to a fenestrule; carina slight, nodes small, sharp, and closely spaced; cells rhomboidal in shape.*

The zoarium is fenestrate; in 10 mm. there are about 24 to 30 branches and 13 to 14 fenestrules. The branches are thin and straight, bifurcating only at distant intervals; they are about 0·2 mm. in width, and bear two rows of zooecial apertures, separated by a slight, low but distinct carina, on which there is a single row of small, sharp nodes; these nodes are spaced 0·19 to 0·24 mm. apart, there being about 47 nodes in 10 mm. The zooecial apertures are rounded, about 0·12 mm. in diameter, and they are surrounded by thin distinct peristomes; there are three to four apertures in the length of one fenestrule and one dissepiment, and about 44 in 10 mm., the distance between the centres of successive apertures being 0·2 to 0·24 mm. The fenestrules are oval to rectangular in outline, and are usually between 0·61 and 0·71 mm. long and 0·15 to 0·22 mm. wide; the dissepiments are 0·06 to 0·12 mm. wide. On the reverse surface both branches and dissepiments are smooth and are evenly rounded, the dissepiments being depressed below the level of the branches. The cells are rhomboidal in outline on the basal plate.

This species is of especial interest because of the shape of its cells, which are similar in outline to the cell shape found in the great majority of Permian species in New South Wales.

Genus HEMITRYPA Phillips, 1841.

Hemitrypa Phillips, 1841, 27; *Hemitrypa* Phillips, Ulrich, 1890, 396, 559; Nikiforova, 1933, 30, 55.

"*Zoaria funnel-shaped or undulating foliar expansions; branches rigid. Zooecia in two ranges, their apertures separated by a moderately developed keel. The latter is elevated at regular intervals into small pillars, which, when the superstructure they support is worn away, appear as spine-like prominences. · The superstructure consists of straight or zig-zag longitudinal bars, of which one is placed over each branch upon the row of pillars and another, usually somewhat thinner, suspended midway between the branches. These bars are then connected by transverse processes, so as to leave regular, small, generally hexagonal openings, corresponding in number and position with the zooecial apertures beneath them.*"   (Ulrich, 1890, 396.)

Genotype: *Hemitrypa oculata* Phillips, 1841.

Range: Devonian to Carboniferous, ? Permian.

The only previous record of the occurrence of this distinctive genus in Australia was made by Lonsdale, who in 1844 described, and in 1845 figured, one species, *Hemitrypa sexangula* Lonsdale, 1844, from the Permian of southern Tasmania; no later description or fresh record of the occurrence of this species has since been made, and Lonsdale's specimens, which formed part of Darwin's collection of fossils from Australia, have long been lost. A second species of this interesting genus occurs in Devonian strata in a railway cutting near Lake Bathurst, New South Wales (specimens F.30170, 30175, Australian Museum Colln.).

HEMITRYPA CLARKEI, n. sp.   Pl. vi, figs. 1, 2.   Text-fig. 46.

Holotype: 6430, Sydney Univ. Colln.

Horizon and locality: Lower Burindi Series, Glen William (holotype); Lower Burindi Series, Hilldale (specimens 7405, 7410, Sydney Univ. Colln.).

Hemitrypa *with fenestrate part fine meshed; 2·5 zooecia to a fenestrule; carina sharp, with nodes which support the superstructure developed at frequent intervals; superstructure a thin regular hexagonal meshwork.*

and they alternate irregularly; they are given off at an angle which varies greatly even in the same specimen, usually between 25° and 55°; a few of the lateral branches themselves become pinnate. There are about 9 lateral branches given off on each side of the midrib in 10 mm.; the distance between the points of origin of successive lateral branches is rather variable, being between 0·8 and 2·3 mm. The lateral branches are connected at intervals by non-poriferous dissepiments, the length of the fenestrules so formed being usually between 0·93 and 1·35 mm., although very short fenestrules about 0·3 mm. long are occasionally developed; the width of the dissepiments is 0·07 to 0·28 mm. Both midrib and lateral branches bear two rows of zooecial apertures, separated by a slight carina; a single row of small, sharp nodes, their spacing about the same as that of the zooecial apertures, occur on this carina. There are usually 3 to 4, sometimes 5, zooecia to a fenestrule, but up to 7 occur along the longer side of the fenestrule adjoining the midrib. The zooecial apertures are circular, 0·08 to 0·11 mm. in diameter, and they often project rather strongly into the fenestrules; there are 29 apertures in 10 mm., the distance between the centres of successive apertures being 0·31 to 0·38 mm. The zooecia themselves are triangular in outline, with strongly developed inferior hemisepta, which are prominent where the reverse of the zoarium has been weathered or broken away and the backs of the zooecia revealed. The reverse surface of the branches is rounded and finely granular.

De Koninck (1877, 169, 170; 1898, 130) described *Dendricopora hardyi* as a new genus and species of pinnate bryozoan from the Carboniferous at Burragood on the Paterson River; his two figures of this species, both natural size, show that it was a much coarser form than *P. konincki*, and according to his description, the midribs and branches showed three rows of zooecia, and there were 10 to 11 zooecia to a fenestrule. *Dendricopora* has usually been listed as a synonym of *Ptilopora*, but if de Koninck was correct in stating that it possessed three rows of zooecia, it is distinct. Prantl (1934, 1935, according to *Zoological Record*, 1936) has recorded species of *Dendricopora* from the Carboniferous of Bohemia.

Fragments of pinnate zoaria are common in the Lower Carboniferous of the northern Hunter River district, and especially at Rouchel Brook; the majority of these appear to be broken pieces of *Ptilopora*, and at least one species besides *P. konincki* occurs at Rouchel Brook; this species is known from a number of specimens which are poorly preserved, but which show that the zooecia were long, narrow and oval, almost rectangular, in outline, lying in two parallel rows along each branch, and quite different in shape to the triangular zooecia of *P. konincki*.

P. konincki is abundant at Rouchel Brook and less common at Glen William, but a specimen from the latter locality was selected as the type as it is much the best preserved specimen examined; in all the material from Rouchel Brook recrystallization of the calcium carbonate of the zoarium has partially obscured the structure.

Genus PENNIRETEPORA d'Orbigny, 1849.

Penniretepora d'Orbigny, 1849, 501; *Penniretepora* d'Orbigny, Bassler, 1935, 20, 165; Crockford, 1942, 110; synonyms: *Pinnatopora* Vine, 1884; *Glauconome* Auct. (not Goldfuss, 1826).

Text-fig. 45.—*Fenestrellina acarinata*, n. sp. Part of the obverse surface of the holotype, × 10.

Text-fig. 46.—*Hemitrypa clarkei*, n. sp. Part of the holotype, weathered from the reverse surface to show the backs of the cells, a cast of the obverse surface, and the hexagonal meshwork which overlies the obverse surface, × 10.

Text-fig. 47.—*Penniretepora osbornei*, n. sp. Cast of part of the obverse surface of the holotype, × 10.

Text-fig. 48.—*Fenestrellina cribriformis*, n. sp. Weathered surface of part of the holotype, × 10.

Text-fig. 49.—*Fenestrellina rouchelis*, n. sp. Weathered surface of part of the holotype, × 10.

Text-fig. 50.—*Fenestrellina propinqua* (de Koninck). Part of the neotype, weathered from the reverse surface to show the backs of the cells and a cast of the obverse surface, × 10.

Text-fig. 51.—*Ptilopora konincki*, n. sp. Part of the holotype, weathered from the reverse surface to show the backs of the cells and a cast of the obverse surface, × 10.

PENNIRETEPORA OSBORNEI, n. sp.   Text-fig. 47.

Holotype: 6428, Sydney Univ. Colln.

Horizon and locality: Lower Burindi Series, Glen William.

Penniretepora *with two zooecia between the origins of successive lateral branches; strong carina with sharp, widely spaced nodes.*

The zoarium is pinnate; the width of the midrib is 0·24 to 0·3 mm., and lateral branches, 0·14 to 0·24 mm. in width, are given off almost opposite at angles of 60° to 70°. The lateral branches are given off at rather regular intervals, 0·68 to 0·8, but usually about 0·72 mm., and there are about 14 in 10 mm. There are two rows of zooecial apertures separated by a strong median carina on both midrib and lateral branches; the carina bears a single row of small sharp nodes spaced 0·57 to 0·67 mm. apart on the midrib and two-thirds of this distance apart on the lateral branches. The apertures are oval, 0·15 × 0·1 mm. in diameter, and are surrounded by slight peristomes; they do not project so as to give the edges of the branch a serrated appearance. The distance between the centres of successive apertures is 0·34 to 0·37 mm., and there are about 28 apertures in 10 mm., there being two apertures between the points of origin of successive lateral branches on each side of the midrib. The reverse surface of the zoarium was rounded and finely granular.

This form is differentiated by its much more closely spaced lateral branches, by the higher carina and more widely spaced nodes, as well as by the lack of dissepiments, from *Ptilopora konincki*, n. sp., with which it is associated at Glen William.

Family RHABDOMESONTIDAE Vine.
Genus STREBLOTRYPA Ulrich, 1890.

Streblotrypa Ulrich, 1890, 403, 665; *Streblotrypa* Ulrich, Bassler, 1929, 66; Crockford, 1944, 168.

STREBLOTRYPA PARALLELA, n. sp.   Pl. iv, fig. 3; Text-figs. 24, 25.

Holotype: 7400, Sydney Univ. Colln.

Horizon and locality: Lower Burindi Series, Hilldale (holotype); Lower Burindi Series, Glen William (6437, Sydney Univ. Colln.); Burindi Series, near Barrington House, Williams River, Barrington Tops (F.42112, Australian Museum Colln.); Lower Kuttung Series, Rouchel Brook (7416, Sydney Univ. Colln.).

Fine Streblotrypa, *with about 15 rows of zooecia; eight small mesopore-like pits in the area behind each aperture; zooecia short, arising from an imaginary axis along the centre of the branch.*

The zoarium is ramose; the branches are straight and very thin, about 1·0 mm. in diameter; lateral branches, which are slightly thinner near their origin, are given off at very distant intervals. There are about 15 rows of zooecial apertures; the apertures are oval, 0·08 × 0·13 mm. in diameter, and they are arranged in regular longitudinal rows, separated by slight longitudinal ridges; and they are also arranged in diagonally intersecting series. There are 29 zooecia in each longitudinal row in 10 mm., the distance between the centres of successive apertures being 0·28 to 0·40 mm. The area behind each aperture, and bounded on each side by the longitudinal ridges, contains about eight tiny mesopore-like pits, arranged generally in three longitudinal rows, with three pits in each of the two outer rows and two in the median row. No acanthopores are developed.

The zooecia are short and diverge sharply from an imaginary axis along the centre of the branch; there is no central bundle of small tubes developed in this species. The cortical zone is about 0·08 mm. thick, and the zooecia, although they bend outwards more sharply in this zone, meet the surface obliquely.

The small dimensions of this form readily distinguish it from any species previously described from Australia; amongst the North American Lower Carboniferous forms this species most closely resembles *S. nicklesi* Ulrich (1890, 667), but it is, however, a coarser species than the American form and differs in the number and arrangement of its mesopore pits.

As well as this common species of *Streblotrypa*, fine ramose Rhabdomesontidae as well as ramose batostomellids are of fairly frequent occurrence in material collected from horizons on which Bryozoa are common in the Lower Burindi and Lower Kuttung of the northern Hunter River district; the specimens are, however, usually poorly preserved, so that only this one species belonging to this family is described here.

<center>Family SULCORETEPORIDAE Bassler, 1935 (restricted).</center>

Cystodictyonidae (pars), Ulrich, 1884, 34; Ulrich, 1890, 385; Sulcoreteporidae (pars), Bassler, 1935, 21.

"*Zoaria consisting of two or three layers of cells grown together back to back, forming thin foliate expansions or triangular branches. Primitive cells semi-cordate or obovate-acuminate in outline, arranged in longitudinal series between vertical double plates. Primitive apertures sub-circular, being somewhat truncated on the posterior side. As growth proceeds the aperture is drawn out shaft-like, forming a tubular vestibule, and the longitudinal plates become obsolete. Superficial aperture with peristome and more or less developed lunarium. Interspaces between zooecia and vestibules occupied by vesicular tissue, the vesicles more or less completely filled with a minutely perforated calcareous deposit near the surface. Margin of zoarium sharp or rounded, and like the basal portion, non-celluliferous.*" Ulrich, 1890, 385 (as Cystodictyonidae Ulrich).

Range: Devonian to Permian.

Ulrich (1884) originally proposed the family Cystodictyonidae to include the genera *Cystodictya, Coscinium, Glyptopora, Prismopora* and *Evactinopora*, and possibly *Rhinopora, Taeniopora* and *Scalaripora*.

Bassler in 1935 drew attention to the fact that *Cystodictya* Ulrich, 1882, is a synonym of *Sulcoretepora* d'Orbigny, 1849, and therefore proposed the new name Sulcoreteporidae for the family.

Bassler referred sixteen genera to this family: *Acrogenia, Ceramella, Coscinium, Dichotrypa, Evactinopora, Glyptopora, Goniocladia, Phractopora, Prismopora, Ptilocella, Ramipora, Scalaripora, Semiopora, Sulcoretepora, Taeniopora* and *Thamnotrypa*. It is here considered that revision of this grouping is necessary, and that many of these genera should be removed from this family and placed as a sub-family of the Fistuliporidae. The reasons for this are as follows:

Sulcoretepora is characterized by a specialized type of cryptostomatous internal structure. The name *Sulcoretepora* was proposed by d'Orbigny with a poor and very inaccurate description—"Cellules placées par lignes dans les sillons longitudinaux, et d'un seul côté de branches simples déprimées, striées en long du côté oppose aux cellules"; "*Flustra parallela* Phillips, Yorkshire, pl. 1, f. 47, 48" was selected as the type. Phillips's (1836) description of this species, which was accompanied by two small figures, is as follows: "Linear, longitudinally and deeply furrowed; cells in the furrows, in quincunx, their apertures oval, prominent; (side furrows without cells). It appears to have been a tubular or folded membrane; the number of rows of cells differs in different specimens. No sign of bifurcation." M'Coy (1845, 198), who referred to this form as "*Vincularia parallela*", gave a brief description, pointing out that zooecial apertures were developed on each side of the zoarium and that the margins of the zoarium were smooth and without pores; later, d'Orbigny, in proposing the new name *Sulcoretepora* for this species, failed to realize that the branches were bifoliate. The only more recent reference which adds any information as to the structure of this form has been made by Ulrich (1884, 36), who briefly described specimens from Kentucky which he believed were identical with Phillips's specimens, and which were considered by him to be congeneric with *Cystodictya ocellata* Ulrich, the genotype of *Cystodictya* Ulrich.

Cystodictya is characterized by its narrow, ribbon-like bifoliate branches, on the surface of which the zooecial apertures are arranged in, usually, regular longitudinal and diagonally intersecting series; lunaria are commonly developed. Internally the zooecia are tubular, at first lying parallel to the mesial lamina and then bending

upwards sharply to meet the surface at almost a right angle; in tangential sections passing through the zoarium close to the mesial lamina the zooecial tubes are arranged "in longitudinal series between vertical plates, to one of which they are laterally attached, while the intervening spaces are occupied by irregularly shaped smaller cells" (Ulrich, 1884, 35). The zooecia in sections cut at this level are semi-cordate in outline; hemisepta are frequently developed; closer to the surface the vesicular tissue between the zooecia is gradually replaced by dense tissue, the interspaces appearing smooth and solid at the surface, sometimes with faint to prominent longitudinal ridges developed between the rows of apertures. The genotype has been figured by Ulrich (1882, Pl. viii, figs. 3, 3a; 1884, Pl. ii, figs. 3, 3a); the tangential section which he figures passes rather close to the surface and does not show the characteristic arrangement of the semi-cordate zooecia between longitudinal vertical plates as well as it is shown in the figures of other species of the genus given by Ulrich and in figures given by more recent workers (Moore, 1929, Pl. 18; McNair, 1937, Pls. x–xiii).

Although this specialized type of internal structure has not been figured in any specimens of *Sulcoretepora parallela* (Phillips) from the type locality in Yorkshire, Ulrich placed specimens which he considered conspecific with this form in *Cystodictya*, and the external appearance of the specimens figured by Phillips, with the zooecia situated in furrows between prominent longitudinal ridges, perhaps also reflects the presence of vertical plates between the rows of zooecia internally, such ridges being also developed strongly in other species, such as *Sulcoretepora bifidiplicata* McNair and *S. obliqua* McNair.

A similar type of internal structure has been shown to exist in some of the other genera referred to the Sulcoreteporidae—in *Dichotrypa* Ulrich, where the zoaria are broad bifoliate fronds, in *Taeniopora* Nicholson and *Semiopora* Hall, and possibly in *Ptilocella* Simpson and *Acrogenia* Hall, which are very similar in their external appearance to *Sulcoretepora* and are classified with it, but whose internal structure does not appear to have been adequately illustrated.

Ulrich's original definition (1884) of the family did not mention the semi-cordate shape of the zooecia or the presence between the rows of zooecia of vertical plates as structures characteristic of the family, though he did describe these at length under his description of the type genus (as *Cystodictya*). In the revised and fuller definition which he gave in 1890, and which is quoted above, these characters are given as typical of the family. As has been pointed out on a previous page, many of the genera previously referred to the Sulcoreteporidae lack the vertical plates between the rows of zooecia, and their zooecia are simple and tubular, not semi-cordate, and are without hemisepta; the classification of these genera has been discussed on a previous page (p. 7). It is here considered that the family Sulcoreteporidae should be restricted to the genera which show the specialized cryptostomatous internal structure of *Sulcoretepora*; the remaining genera should be removed to the Fistuliporidae, of which family they are here considered to form a separate sub-family, the Hexagonellinae.

Genus DICHOTRYPA Ulrich, 1889.

Dichotrypa Ulrich, 1889, 300; Ulrich, 1890, 385, 498.

Sulcoreteporidae with large thin bifoliate expansions, the surface with solid maculae; zooecia at first parallel to the mesial lamina, then bending upwards to the surface; lunaria more or less strongly developed; internal structure as in Sulcoretepora.

Genotype: *Dichotrypa foliata* Ulrich, 1890.

Range: Devonian to Mississippian.

DICHOTRYPA FRAGILIS, n. sp. Pl. iv, fig. 2; Text-figs. 27, 28.

Holotype: F.42112A, Australian Museum Colln.

Horizon and locality: Burindi Series, near Barrington House, Williams River, Barrington Tops.

Zoarium a spreading bifoliate frond with long, elliptical, depressed maculae; zooecia short, with distinct lunaria, and separated by fine vesicular tissue, with vertical plates between the rows of zooecia.

The zoaria are spreading bifoliate fronds reaching a maximum size of about 3·5 × 2 cm.; they are about 0·55 mm. in their maximum thickness, and are extremely thin near the periphery. The zoaria appear to arise from a small base near the centre of each colony, above which the colony spreads out rapidly; in each specimen it is the upper surface of the colony which is exposed, but one specimen, the holotype, shows a small protuberance in the centre where the colony appears to have been crushed against the base beneath, and in each specimen the zooecia radiate from the centre of the colony. The surface is marked by long, elliptical, slightly depressed maculae, usually about 4 to 7 mm. long, though they may be shorter, and from 1 to 2 mm. in their greatest width; the zoarium was so thin in the position of the maculae that they now usually appear as elongate spaces, but the thin solid tissue of the maculae remains in one or two places.

The zooecial apertures are small, and they are usually indented slightly by lunaria; their measurements are: a, 0·22 to 0·24 mm.; b, 0·22 to 0·25 mm.; c, 0·08 mm.; d, 0·16 mm. The apertures are surrounded by high peristomes, highest on the side on which the lunarium is developed—this is usually the side closer to the centre of the zoarium; the lunaria are thin, and they occupy about one-third of the circumference of each zooecial tube, but unfortunately crushing of the zoarium has distorted many of the zooecial apertures. There are about 34 zooecia in 7 sq. mm.; they are arranged in more or less regular rows radiating from the centre of the zoarium. At the surface the interspaces between the zooecia are smooth and solid; unfortunately, slides made of this form did not satisfactorily show the internal structure—the zoarium was slightly recrystallized, and was also rather crushed; the internal structure is, however, shown well on slightly weathered surfaces of the zoarium; the zooecial tubes are short; they lie back to back on either side of the mesial lamina for a short distance, and then curve sharply upwards to meet the surface perpendicularly; they are arranged in rows (which radiate from the centre of the zoarium) between vertical plates, and close to the mesial lamina rather numerous small vesicles occur between and above the zooecia; as the surface is approached these are replaced by a very thin layer of dense tissue.

In the largest specimen, the holotype, the zoarium is practically flat, but in a second specimen (F.42112B, Australian Museum Colln.) the zoarium is thrown up into two broad, deep folds along one edge.

This species is referred with some hesitation to *Dichotrypa* as, although in essentials it possesses the characters of this genus, it is unlike described species of *Dichotrypa* in its very elongate maculae, which give it a marked superficial resemblance to species of *Ceramella* and to fragmentary specimens of *Glyptopora*. From *Glyptopora* it is distinguished by the form of its zoarium, since, although one of the zoaria is strongly folded along one edge, the specimens, despite their small size, appear to be almost complete, and there is no tendency to form a complex zoarium composed of a number of cup-shaped masses such as that found in *Glyptopora*. From *Ceramella* it is distinguished by the well-developed lunaria which are clearly shown in some of the zooecial tubes, and the internal structure appears to be rather different from that found in either *Ceramella* or *Glyptopora*. From *Coscinium* it is distinguished by possessing solid maculae instead of open fenestrae bordered by a narrow solid edge. It therefore seems more closely related to *Dichotrypa* than to any of these three genera, since the shape of the maculae, though it is occasionally persistent and characteristic of a generic group, is of far less importance than the differences from other genera mentioned above.

Ceramella casei McNair, 1937, from the Middle Devonian Traverse Group of Michigan, resembles this species in its general external appearance; it also is an extremely thin bifoliate expansion, with similar elongate maculae with small zooecial apertures separated by solid tissue at the surface, but with the zooecia separated by vesicular tissue close to the centre of the zoarium; it differs from *Dichotrypa fragilis*, however, in the details of its size and structure, including the absence of lunaria.

SUMMARY.

The Bryozoa described in this paper are collections from the Lower Carboniferous of Queensland and from the Lower and Upper Burindi Series and the Lower Kuttung Series (Lower Carboniferous) of New South Wales; these collections contained representatives of a number of genera common in the Lower Carboniferous of Europe and North America but not previously known to occur in rocks of this age in eastern Australia.

BIBLIOGRAPHY.

BASSLER, R. S., 1929.—The Permian Bryozoa of Timor. *Paläontologie von Timor*, xvi Lief., xxviii.

————, 1935.—Fossilium Catalogus, I: Animalia, pars 67; Bryozoa.

————, 1941.—Generic Descriptions of Upper Paleozoic Bryozoa. *J. Wash. Acad. Sci.*, 31 (5): 173.

BENSON, W. N., 1921.—A Census and Index of the Lower Carboniferous Burindi Fauna of New South Wales. *Rec. Geol. Surv. N.S.W.*, 10 (2): 12.

BRYAN, W. H., and JONES, O. A., 1944.—A Revised Glossary of Queensland Stratigraphy. *Univ. Qd. Pap., Dept. Geol.*, N.S., 2 (11).

CHAPMAN, F., 1920.—Lower Carboniferous Limestone Fossils from New South Wales. *Proc. Linn. Soc. N.S.W.*, 45 (3): 364.

CONDRA, G. A., and ELIAS, M. K., 1944.—Study and Revision of *Archimedes*. *Geol. Soc. Amer.*, Special Papers, 53.

CROCKFORD, JOAN, 1942.—Bryozoa from the Silurian and Devonian of New South Wales. *J. Roy. Soc. N.S.W.*, 75 (for 1941): 104.

————, 1943.—Permian Bryozoa from Eastern Australia. Part 3. Batostomellidae and Fenestrellinidae from Queensland, New South Wales, and Tasmania. *Ibid.*, 76 (for 1942): 258.

————, 1944.—Bryozoa from the Permian of Western Australia, Part i. Cyclostomata and Cryptostomata from the North West Basin and Kimberley District. *Proc. Linn. Soc. N.S.W.*, 69 (3-4): 139.

————, 1945.—Stenoporids from the Permian of New South Wales and Tasmania. *Ibid.*, 70 (1-2): 9-24.

DANA, J. D., 1849.—Fossils of New South Wales. In Wilkes' U.S. Exploring Expedition, X, Geology, Appendix and Atlas.

DUNCAN, HELEN, 1939.—Trepostomatous Bryozoa from the Traverse Group of Michigan. *Mich. Univ. Mus. Paleont., Contr.*, 5 (10): 171.

EASTON, W., 1943.—The Fauna of the Pitkin Limestone of Arkansas. *J. Paleont.*, 17 (2): 125.

————, 1944.—Review in *J. Paleont.*, 18 (4): 405.

ETHERIDGE, R., jnr., 1876.—Carboniferous and Post-Tertiary Polyzoa. *Geol. Mag., Lond.*, N.S., Dec. 2, 3: 522.

————, 1892.—*In* Jack, R. L., and Etheridge, R., jnr., Geology and Palaeontology of Queensland and New Guinea. *Qd. Geol. Surv.*, Publ. No. 92.

————, 1900.—Corals from the Coral Limestone of Lion Creek, Stanwell, near Rockhampton. *Qd. Geol. Surv.*, Bull. 12.

HALL, J., 1857.—Observations on the Genus *Archimedes* or *Fenestella*, with Descriptions of Species. *Proc. Amer. Assoc. Adv. Sci.*, 10, 1856: 176.

HILL, DOROTHY, 1934.—The Lower Carboniferous Corals of Australia. *Proc. Roy. Soc. Qd.*, 45 (12): 63.

————, 1943.—A Re-interpretation of the Australian Palaeozoic Record, based on a Study of the Rugose Corals. *Ibid.*, 56 (6): 53.

KONINCK, L. G. DE, 1877.—Recherches sur les fossiles paléozoiques de la Nouvelle Galle de Sud. *Mém. Soc. Roy. Sci. Liége*, (2) 8: 1. (Reprinted in English in *Mem. Geol. Surv., N.S.W., Palaeont.*, 6.)

LEE, G. W., 1912.—The British Carboniferous Trepostomata. *Mem. Geol. Surv., G.B., Palaeont.*, 1 (3): 135.

M'COY, F., 1845.—Synopsis of the Carboniferous Limestone Fossils of Ireland. University Press, Dublin, 1845.

————, 1847.—On the Fossil Botany and Zoology of the Rocks associated with the Coal in Australia. *Ann. Mag. Nat. Hist.*, (1) 20: 226.

————, 1849.—On Some New Genera and Species of Palaeozoic Corals and Foraminifera. *Ibid.*, (2) 3: 119.

McNAIR, A., 1937.—Cryptostomatous Bryozoa from the Middle Devonian Traverse Group of Michigan. *Mich. Univ. Mus. Paleont. Contr.*, 5 (9): 103.

MOORE, R. C., 1929.—A Bryozoan Faunule from the Upper Graham Formation (Pennsylvanian) of North-Central Texas. Part i. *J. Paleont.*, 3 (1):1. Part ii. *Ibid.*, 3 (2):121.

————, and DUDLEY, RUTH, 1944.—Cheilotrypid Bryozoa from Pennsylvanian and Permian Rocks of the Midcontinent Region. *St. Geol. Surv. Kans.*, Bull., 52 (6): 229.

NICHOLSON, H. A., 1874.—Descriptions of Species of *Chaetetes* from the Lower Silurian Rocks of North America. *Quart. J. Geol. Soc. Lond.*, 30: 499.

————, and ETHERIDGE, R., jnr., 1886.—On the Tasmanian and Australian Species of the Genus *Stenopora*. *Ann. Mag. Nat. Hist.*, (5) 17: 173.

NICKLES, J., and BASSLER, R. S., 1900.—A Synopsis of American Fossil Bryozoa, including Bibliography and Synonymy. *U.S. Geol. Surv.*, Bull. 173.

NIKIFOROVA, A. I., 1933.—Middle Carboniferous Bryozoa of the Donetz Basin. *Trans. Un. Geol. Prosp. Serv. U.S.S.R.*, Fasc. 364.

ORBIGNY, A. d', 1849.—Sur Quelques Genres Nouveaux de Mollusques Bryozoaires. *Rev. Mag. Zool.*, (2) 1: 499.

OWEN, D. D., 1842.—Regarding Human Footprints in Solid Limestone. *Amer. J. Sci.*, (1) 43: 14.

PHILLIPS, J., 1827.—The Geology of Yorkshire, Vol. 2.

————, 1841.—Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon, and · West Somerset. London, 1841.

RAGGATT, H. G., and FLETCHER, H. O., 1937.—A Contribution to the Permian-Upper Carboniferous Problem and an Analysis of the Fauna of the Upper Palaeozoic (Permian) of North-West Basin, Western Australia. *Rec. Aust. Mus.*, 20: 150-184.

SHULGA-NESTERENKO, M. J., 1933.—Bryozoa from the Coal-bearing and Subjacent Series of Pechora Land: *Goniocladia* Etheridge and *Ramipora* Toula, Carboniferous and Permian Representatives of the Family Cystodictyonidae. *Trans. Un. Geol. Prosp. Serv. U.S.S.R.*, · Fasc. 259.

TOULA, F., 1875.—Permo-Carbon-Fossilien von der Westkuste von Spitzbergen. Leonhard und Bonn's Neues Jahrbuch fur Mineralogie, 1875: 225.

ULRICH, E. O., 1882-5.—American Palaeozoic Bryozoa. Papers in *J. Cincinn. Soc. Nat. Hist.*, Vols. 5-8.

————, 1890.—Paleozoic Bryozoa. *Geol. Surv. Ill.*, Vol. 8.

————, 1896.—In Zitel's Text-book of Palaeontology, English Edition, Vol. 1.

VOISEY, A. H., 1938.—The Upper Palaeozoic Rocks in the Neighbourhood of Taree, N.S.W. *Proc. Linn. Soc. N.S.W.*, 63: 453-462.

WHITEHOUSE, F. W., 1929.—*Abstract of Proceedings, Proc. Roy. Soc. Qd.*, 41: xii.

EXPLANATION OF PLATES I-VI.

Plate i.

Fig. 1.—*Fenestrellina yarrolensis*, n. sp. Obverse surface of the holotype, × 10.

Fig. 2.—*Polypora sulcifera*, n. sp. Obverse surface of the holotype, × 10.

Figs. 3-6.—*Evactinopora irregularis*, n. sp. Holotype. 3. Part of the surface of one of the rays, showing the elongate depressed maculae and the zooecial apertures, some of these being indented by lunaria, × 10. 4. Upper edge of the zoarium, natural size. 5. Lateral view of the zoarium, natural size. 6. Base of the zoarium, natural size.

Plate ii.

Figs. 1-2.—*Archimedes regina*, n. sp. Holotype. 1. Zoarium, natural size. 2. Obverse surface of portion of the meshwork, × 10.

Figs. 3-6.—*Archimedes spiralis*, n. sp. Holotype. 3. One of the fractured rootlets, which repeatedly forked at its distal end, × 10. 4. Lower end of the shaft, showing the rapid increase in diameter of the shaft above the second volution, where the shaft is joined by a ring of rootlets, × 2·5. 5. The shaft, showing in direction of growth above the fracture between the sixth and seventh volutions, and the broken bases of the rootlets developed on the under side of the shaft below the fracture; the frond is broken off at the edge of the flange throughout the zoarium; natural size. 6. Surface of the zoarium at the level of the ninth volution, showing the fractured ends of the branches of the meshwork, the direction of the striae of the fibrous tissue of the shaft, and the overgrowth of the shaft tissue over the broken ends of the branches on the upper side of the shaft.

Plate iii.

Figs. 1-2.—*Fistulamina malmoensis*, n. sp. Holotype. 1. Part of the zoarium, × 2·5. 2. Surface, showing apertures with peristomes and strongly-developed lunaria, × 10.

Fig. 3.—*Penniretepora fragilis*, n. sp. Obverse surface of the holotype, × 10.

Figs. 4-5.—*Ramipora (Ramiporella) flexuosa*, n. sp. 4. Obverse surface of the holotype, × 10. 5. Spreading base of a zoarium (F5768F, Qd. Univ. Colln.) from which three branches arise, two of these branches being broken off just above the base, × 10.

Plate iv.

Fig. 1.—*Evactinopora trifoliata*, n. sp. Holotype, showing two of the three vertical rays, lightly attached at their bases to a *Spirifer*, natural size.

Fig. 2.—*Dichotrypa fragilis*, n. sp. Upper surface of the holotype (a), natural size.

Fig. 3.—*Streblotrypa parallela*, n. sp. Part of the holotype, × 10. Near the centre of the photograph the zooecial tubes can be seen diverging from a fine line down the centre of the zoarium.

Fig. 4.—*Fistulipora mirari*, n. sp. Weathered surface of the holotype, × 10.

Figs. 5-6.—*Fistulamina inornata*, n. sp. Holotype. 5. Zoarium × 2·5. 6. Part of the surface of the zoarium, × 10.

Plate v.

Fig. 1.—*Ramipora (Ramiporalia) bifurcata*, n. sp. Holotype, natural size.

Fig. 2.—*Goniocladia parva*, n. sp. Part of the holotype, × 10.

Figs. 3-5.—*Goniocladia laxa* (de Koninck). 3. Part of a large zoarium (5424, Sydney Univ. Colln.), natural size. 4. A small portion of this same specimen, showing the reverse surface of a branch and, where weathered, showing the zooecia and vesicles, × 10. 5. Obverse surface of another zoarium (5424B, Sydney Univ. Colln.), × 10.

Plate vi.

Figs. 1-2.—*Hemitrypa clarkei*, n. sp. 1. Part of the surface of the holotype, showing the fenestrate zoarium and in the upper left-hand corner part of the finer hexagonal meshwork of the superstructure which is developed above the obverse surface, × 10. 2. A similar view of a second specimen (6430B, Sydney Univ. Colln.), × 10.

Fig. 3.—*Fenestrellina acarinata*, n. sp. Holotype, × 10.

Fig. 4.—*Fenestrellina propinqua* (de Koninck). Neotype, × 10.

Fig. 5.—*Ptilopora koninoki*, n. sp. Holotype, × 10.

THE UTILIZATION OF FUMARATE AND MALATE BY *ESCHERICHIA COLI* IN THE PRESENCE OF MOLECULAR HYDROGEN.

By June Lascelles, Linnean Macleay Fellow of the Society in Biochemistry, and J. L. Still, Department of Biochemistry, University of Sydney.

(Two Text-figures.)

[Read 30th April, 1947.]

Introduction.

The reduction of fumarate by molecular hydrogen in the presence of washed suspensions of bacteria was first observed by Stephenson and Stickland (1931) using *Escherichia coli*. The phenomenon was studied by Krebs (1937) using a different strain of *E. coli*.

Fischer and Eysenbach (1937), using cell-free extracts of a strain of yeast, which did not appear to contain succinic dehydrogenase, showed that fumarate could be reduced enzymically with the hydrogen donated by certain reduced dyes of low E'_0 values. Later, Fischer, Roedig and Rauch (1939) obtained evidence that the enzyme responsible for this reaction, fumarate hydrogenase, was a flavoprotein.

Claren (1938), using washed suspensions of luminous bacteria, showed that fumarate was a hydrogen acceptor in the presence of molecular hydrogen, succinate being the product of the reaction. Under similar conditions, malate was also an acceptor. He observed that in these suspensions the Knallgas reaction did not occur in the absence of fumarate and concluded that the role of fumarate was catalytic. Succinate had the same effect as fumarate.

Hoberman and Rittenberg (1943) observed that hydrogenase of suspensions of *Proteus vulgaris*, as measured by the exchange reaction with heavy hydrogen, was inactivated by molecular oxygen and reactivated by incubation with fumarate, succinate and glucose.

The present study was undertaken to find out the relationship between hydrogenase and the enzyme systems activating fumarate and malate in washed suspensions of *E. coli*.

Methods.

The organisms were grown and suspensions prepared as described previously (Lascelles and Still, 1946a). Suspensions of about 5–7 mg./ml. dry weight were found to be most satisfactory.

In many instances experiments were carried out using suspensions treated with toluene as well as with normal suspensions. This treatment consisted in incubation of the cells with toluene for at least 2 hours in an atmosphere of hydrogen at 38°C. Similar preparations could be obtained by keeping the cells under hydrogen with toluene for 16 hours at room temperature, or, for a longer period, in the refrigerator. One effect of toluene was to minimize the reduction of fumarate by donators within the cells.

Some experiments were carried out with cell-free preparations of *E. coli*. These were prepared as previously described (Back, Lascelles and Still, 1946), using the technique of Kalnitsky, Utter and Werkman (1945).

Estimations of succinic acid were carried out by the method of Krebs (1937), after extraction of the acid from the reaction mixture with ether. Fumarate was estimated by the method of Krebs, Smyth and Evans (1940).

E

Otherwise, the techniques used were those described in another paper (Lascelles and Still, 1946a).

THE REDUCTION OF FUMARATE.

Effect of Variation of H-ion Concentration.—The optimum pH using phosphate buffers was 6·0 for normal and toluene treated cells. Phthalate buffers were inhibitory, but this inhibition was not removed by addition of phosphate. Using cell-free extracts, the optimum pH was 6·8. The inhibitory action of phthalate was more marked in the instance of the extract. Acetate buffers of the same pH were not inhibitory.

The Course of the Reaction.—This varied with the cell preparation used. In the instance of the normal cells, the hydrogen uptake corresponded with about 60% of the theoretical uptake required for the complete reduction of the added fumarate to succinate. Analysis showed that approximately 90% of the fumarate disappearing was recoverable as succinate.

In the absence of KOH in the centre well of the manometer vessel, evolution of CO_2 was demonstrable. This evolution of CO_2 was most noticeable in an atmosphere of nitrogen. Krebs (1937) has studied this phenomenon in some detail.
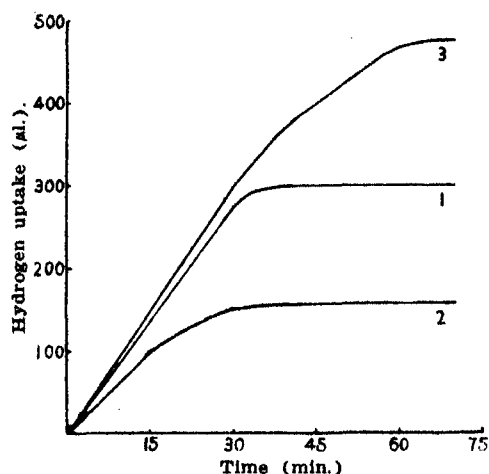
Fig. 1.—Course of hydrogen uptake in the presence of fumarate and malate.

Each manometer vessel contained : 1·0 ml. suspension dry wt. 7·4 mg./ml., 1·5 ml. M/5 phosphate buffer pH 6·0.   0·1 ml. M/5 fumarate and/or 0·1 ml. M/5 dl-malate was in the side arm.   Distilled water was added to make a final volume of 3·0 ml.   In the centre well was 0·2 ml. 20% KOH.

Curve 1.—Course of hydrogen uptake in the presence of M/150 fumarate.

Curve 2.—Course of hydrogen uptake in the presence of M/150 dl-malate.

Curve 3.—Course of hydrogen uptake in the presence of M/150 fumarate and M/150 dl-malate.

Using toluene-treated cells, the hydrogen uptake corresponded with 95–100% of the amount required for complete reduction of the fumarate to succinate (see Figure 1). Analysis showed that 95–100% of the fumarate disappearing was recoverable as succinate. Thus treatment with toluene eliminated most of the blank reduction of fumarate by hydrogen donators remaining in the washed cells. In addition, toluene treatment markedly accelerated the rate of hydrogen uptake in the presence of fumarate (see Table 1).

The toluene-treated cells did not show an evolution of CO_2, in the presence or absence of fumarate. The cell-free extracts behaved like the toluene-treated cells with respect to the correspondnce of hydrogen uptake to the amount of fumarate reduced to succinate; nor did these preparations show an evolution of CO_2.

It was shown that the reduction of methylene blue in the presence of succinate was greatly inhibited after the cells had been treated with toluene as described above.

TABLE 1.

The Effect of Treatment of Suspensions with Toluene.

Each manometer vessel contained 1·0 ml. suspension, 5·3 mg./ml. dry wt. 1·5 ml. M/5 phosphate pH 6·0 ; in the side arm was 0·1 ml. M/10 fumarate. Distilled water was added to make a final volume in each of 3·0 ml. In the centre well was 0·2 ml. 20% KOH.

Toluene Treatment.	Time of Incubation in Hydrogen.	Hydrogen Uptake (µl.). (Min.)					Theoretical Hydrogen Uptake.	Percentage Acceleration by Toluene (20').
		20	40	60	80	90		
—	Nil	32	45	103	112	112	224	—
—	120 min.	36	76	106	112	112	,,	---
+	120 ,,	83	137	197	204	204	,,	130

Concentration of Fumarate.—The maximum rate of hydrogen uptake was obtained with M/300 fumarate, using normal cells, toluene-treated cells or the extract.

Artificial Carriers.—Unlike the reduction of nitrite and hydroxylamine by this strain of *E. coli* (Lascelles and Still, 1946b), reduction of fumarate by molecular hydrogen was independent of added carriers. The addition of cresyl blue, methylene blue or nile blue did not accelerate the hydrogen uptake. Benzyl viologen in concentration 0·002% did increase the rate of hydrogen uptake by about 50%. This was observed in the extracts also. As in the instance of nitrite and hydroxylamine reduction, this may be partly non-enzymic.

Dilution of the Suspensions.—The rate of hydrogen uptake in the presence of fumarate fell off sharply on diluting the suspensions. The activity of the diluted suspensions could be fully restored by the addition of boiled suspension. A preparation of diphosphopyridine nucleotide (DPN) obtained by the method of Williamson and Green (1940) was also active. Manganous ions in a concentration of M/300 restored some of the lost activity, but not to such a marked extent as the boiled suspensions or the DPN preparations. The addition of both DPN and manganous ions restored all the activity of the diluted suspensions.

Addition of M/3,000 manganous ions, M/300 magnesium ions, ferrous ions (as ferrous ammonium citrate) or of M/1,000 muscle adenylic acid did not result in any stimulation of the rate of hydrogen uptake by the diluted suspensions.

This problem will be studied at greater length using cell-free extracts of the bacteria.

Action of Inhibitors.—M/100 cyanide, M/50 hydroxylamine, M/50 hydrazine, and M/100 arsenite did not inhibit appreciably the hydrogen uptake in the presence of fumarate. In all cases the inhibitor was incubated with the cells or extract prior to addition of the fumarate.

Sodium malonate: M/30 malonate inhibited the system by about 20% using normal cells. The inhibition was much more marked after the cells had been treated with toluene and also with the cell-free extract. In these instances the inhibition was 50–70%. The degree of inhibition varied only slightly with variation in concentration of fumarate.

Sodium selenite: M/100 sodium selenite appeared to inhibit the hydrogen-fumarate system, especially with toluene-treated cells, but this compound was itself changed by the bacteria, as shown by the darkening in colour and the generation of a foul odour, suggesting selenium hydride.

Sodium fluoride: M/50 sodium fluoride was inhibitory to the extent of 40–50% using toluene-treated cells; the degree of inhibition was slightly less with normal cells and with the extracts. The effect was independent of the concentration of added magnesium ions.

Sodium pyrophosphate: M/50 pyrophosphate inhibited the toluene-treated cells by about 60%. The reaction in normal cells and in the extract was not inhibited appreciably. The inhibition was independent of the concentration of fumarate.

Carbon monoxide: This inhibitor was used in gas mixtures of hydrogen and carbon monoxide in the ratio $H_2/CO = 1:4$; this partial pressure of carbon monoxide

inhibited the uptake of hydrogen in the presence of fumarate by only 30%. The control experiments were carried out in atmospheres of hydrogen and nitrogen in the ratio of 1:4.

Sodium azide: M/100 sodium azide inhibited the hydrogen fumarate reaction in normal cells by about 30%; however, with the toluene-treated suspensions and in the extract, no inhibition was observed, even with M/30 azide.

Nitrophenols: The effect of certain nitrophenols was markedly changed by toluene treatment of the cells.

The toluene-treated cells and the cell-free extract were not inhibited by any of the four nitrophenols used. However, the rate of hydrogen uptake in the presence of fumarate with normal cells was almost completely inhibited by M/1,000 2:4-dinitrophenol, and partially inhibited by M/1,000 m-nitrophenol and p-nitrophenol, as shown in Table 2.

The action of o-nitrophenol was exceptional in that it brought about a marked increase in the rate of hydrogen uptake. In the absence of fumarate, these nitrophenols always caused a very small hydrogen uptake, not observed in their absence. This was not sufficient to account for the acceleration of hydrogen uptake by o-nitrophenol in the presence of fumarate.

TABLE 2.

Effect of Nitrophenols on Hydrogen Uptake in the Presence of Fumarate.

Contents of vessels as before. Suspension, dry wt. 6·3 mg./ml. Nitrophenols were in contact with the cells during the equilibration period. 0·1 ml. M/4 fumarate was added from the side arm at zero. The toluene cells were stored with toluene for 60 hours at 5° C. in an atmosphere of hydrogen.

Toluene Treatment	Concentration of Fumarate.	Nitrophenol.	Hydrogen Uptake (μl.). (Min.)			Percentage Change 40 Min.
			10	40	60	
---	M/120	Nil	38	207	343	---
,,	,,	M/1000 DNP	0	3	9	- 99
---	,,	M/1000 m-NP	37	179	283	- 14
---	,,	M/1000 o-NP	92	334	450	+69
,,	,,	M/1000 p-NP	8	104	163	- 50
+	,,	Nil	117	376	504	---
+	,,	M/1000 DNP	113	380	515	0
+	,,	M/1000 m-NP	114	392	534	+ 4
+	,,	M/1000 o-NP	113	378	511	0
+	,,	M/1000 p-NP	124	411	548	+10

Ortho-phenanthroline: Gaffron (1945) has shown that o-phenanthroline inhibits the adaptation reaction and photoreduction in *Scenedesmus* by about 50%; this compound also stabilizes the adapted cells against reversion under the influence of strong light.

The uptake of molecular hydrogen in the presence of fumarate was inhibited from 50-70% by M/500 o-phenanthroline. The same results were obtained with normal cells, toluene-treated cells, and with the extract. Shaking the cells or extract in oxygen in the presence of this inhibitor prior to determination of the hydrogen-fumarate activity (by replacement of the oxygen with hydrogen, and addition of fumarate to the reaction mixture) did not increase the inhibition.

Addition of M/300 ferrous ammonium citrate, or M/300 manganese sulphate or M/300 zinc sulphate to the cells or to the extract, after they had been shaken in hydrogen in the presence of M/500 o-phenanthroline, resulted in a partial reversal of the inhibition (see Table 3).

M/300 magnesium chloride and M/300 calcium chloride were ineffective.

Ferrous ions and zinc ions are known to form complexes with o-phenanthroline (Sandell, 1944).

A study was made of this inhibitor on other enzymic reactions involving molecular hydrogen, using the same strain of *E. coli*.

With methylene blue as acceptor, M/500 o-phenanthroline caused a slight acceleration in the rate of hydrogen uptake, when the methylene blue was added to the cells after

TABLE 3.

The Reversal of Inhibition by o-Phenanthroline.

Each vessel filled as before. Cells had been treated with toluene ; dry wt. was 5·0 mg./ml.
o-Phenanthroline (M/500) was in contact with the cells during the equilibration period of 10 minutes.
In the side arms were 0·1 ml. M/4 fumarate and 0·1 ml. of M/10 metallic salt. The contents of
the side arms were tipped into the main compartment at zero time.

Metallic Salt.	Concentration of o-Phenanthroline.	Hydrogen Uptake (μl.). 60 Min.	Percentage Inhibition by o-Phenanthroline.
Nil	0	223	—
Nil	M/500	47	79
M/300 ferrous ammonium citrate	0	217	—
Do.	M/500	151	32
M/300 MnSO₄	0	214	—
Do.	M/500	168	25
M/300 ZnSO₄	0	216	—
Do.	M/500	160	28

they had been shaking in hydrogen in the presence of o-phenanthroline. But if the
cells had been shaken in oxygen in the presence of o-phenanthroline subsequent deter-
mination of the rate of hydrogen uptake in the presence of methylene blue showed that
o-phenanthroline now inhibited by about 80%. It was shown that the cells did not
form an inhibitory compound while shaking with o-phenanthroline in an atmosphere of
oxygen. Thus a suspension of *E. coli* was shaken with phosphate buffer and M/200
o-phenanthroline in an atmosphere of oxygen at 38°C. for 30 minutes; the cells were
then removed from the reaction mixture by centrifugation, and aliquots of the super-
natant were tested for their action on the hydrogen-methylene blue system with fresh
cells. No inhibition was observed. But if the hydrogen-methylene blue reaction were
carried out on the cells which had been shaken in oxygen with o-phenanthroline, strong
inhibition was obtained. Control experiments were performed on suspensions which had
been shaken in oxygen in the absence of o-phenanthroline.

The Knallgas reaction was inhibited by about 90% by M/500 o-phenanthroline. Gas
mixtures containing H_2/O_2 in the ratio of 90/10 were used. Controls containing nitrogen
instead of oxygen showed negligible uptakes of gas. This inhibition of the Knallgas
reaction was partially reversed by M/300 zinc sulphate; this was added to the cells after
they had been shaking with the gas mixture for 30 minutes in the presence of
o-phenanthroline. Manganous ions and ferrous ions were not used, due to the blank O_2
uptake in the presence of these ions.

The rate of hydrogen uptake in the presence of potassium nitrate was inhibited
from 50–60% by M/500 o-phenanthroline. This inhibition was partially reversed by
M/300 ferrous ammonium citrate, MnSO₄ and ZnSO₄ under the same conditions already
described for the reduction of fumarate.

It is not possible yet to decide whether inhibition by o-phenanthroline denotes the
participation of a metal in the catalytic systems.

Sodium iodoacetate: M/1,000 iodoacetate inhibited hydrogen uptake with fumarate
by 98% and M/5,000 by 80%.

The Effect of Molecular Oxygen.—In previous studies of systems involving hydro-
genase, it has been found that shaking of the cells with oxygen inactivates some part
of the system (Lascelles and Still, 1946a). The reduction of fumarate by molecular
hydrogen was also inhibited by previous incubation in oxygen.

The inhibitory effect obtained by preliminary incubation in oxygen was much more
marked in the cell-free extract.

The Effect of Succinate and Maleate.—The effect of addition of these C_4-dicarboxylic
acids on the hydrogen-fumarate reaction is summarized in Table 4.

Thus, under the conditions of these experiments, succinate, the product of the
reduction, did not inhibit the forward reaction when added initially. The system does
not reduce the stereo-isomer, maleic acid, under the conditions suitable for the reduction
of fumarate. Nor is maleic acid an inhibitor of the reduction of fumarate.

TABLE 4.

Effect of Addition of Succinate and Maleate.

Contents of vessels as before. Suspension, dry wt. 7·4 mg./ml. Fumarate and other
additions made from the side arm at zero time.

Concentration of Fumarate.	Additions.	Hydrogen Uptake (μl.). Min.		
		15	40	70
M/150	Nil	135	299	299
0	M/30 maleate	0	+2	+8
M/150	,,	124	316	318
0	M/30 succinate	+2	+4	+6
M/150	,,	135	265	300

THE REDUCTION OF MALATE.

Quastel and Whetham (1924) showed that washed suspensions of *E. coli* contained
the enzyme, fumarase. It was considered likely that, in the present investigation,
addition of malate to the washed suspensions would result in uptake of hydrogen. This
was shown to occur under much the same conditions as held for the reduction of
fumarate.

H-ion Concentration.—The optimum pH for the hydrogen-malate reaction was 6·0
with normal cells, and with the extract was 6·8.

The Course of the Reaction.—In normal cells, the hydrogen uptake per molecule of
dl-malate added was about 30% of the theoretical amount required for the reduction of
the *dl*-malate *via* fumarate to succinate.

In the extract, the uptake corresponded with 50% of that required for complete
reduction of the *dl*-malate to succinate. These findings suggested that only one of the
isomers in the *dl*-malate had been activated by the bacteria. Other workers have shown
that fumarase from animal and bacterial sources is specific for *l*-malic acid and fumaric
acid only.
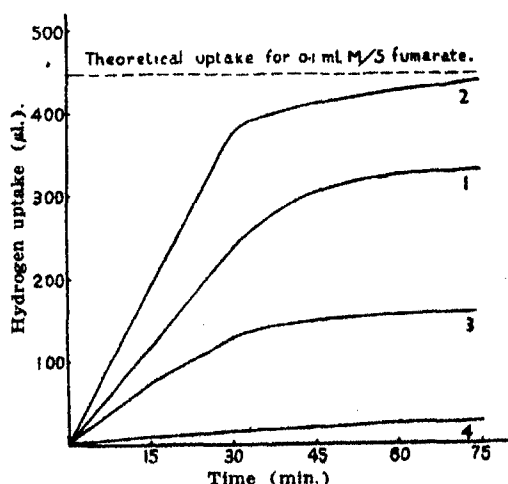
Fig. 2.—Course of hydrogen uptake in the presence of fumarate and malate with untreated
and toluene treated cells.

Contents of vessels as in Figure 1; suspension, dry wt. 7·7 mg./ml.

Curve 1.—Course of hydrogen uptake in the presence of M/150 fumarate; cells kept in an
atmosphere of hydrogen for sixteen hours at 21°C.

Curve 2.—Course of hydrogen uptake in the presence of M/150 fumarate; cells kept in an
atmosphere of hydrogen with toluene for sixteen hours at 21°C.

Curve 3.—Course of hydrogen uptake in the presence of M/150 *dl*-malate; cells kept in
an atmosphere of hydrogen for sixteen hours at 21°C.

Curve 4.—Course of hydrogen uptake in the presence of M/150 *dl*-malate; cells kept in an
atmosphere of hydrogen with toluene for sixteen hours at 21°C.

Figure 1 shows the course of hydrogen uptake by normal cells in the presence of *dl*-malate and fumarate, separately and together.

Toluene treatment inhibited the hydrogen uptake in the presence of *dl*-malate almost completely; under the same conditions, the rate of hydrogen uptake in the presence of fumarate was markedly accelerated. Woolf (1929) showed that 2% cyclohexanol, after incubation with suspensions of *E. coli* for 15 hours, inhibited fumarase completely.

This action of toluene made it possible to examine the properties of the hydrogen-fumarate system uncomplicated by the fumarate-malate equilibrium.

Figure 2 compares the course of hydrogen uptake by toluene-treated cells and normal cells, in the presence of fumarate or *dl*-malate.

Concentration of dl-*Malate.*—The optimum concentration of *dl*-malate was found to be M/100 or greater.

Dilution of the Suspensions.—The hydrogen-malate system showed marked loss in activity when the suspensions were diluted. This system appeared to be more sensitive to dilution than the hydrogen-fumarate system. However, restoration of the lost activity was obtained under the same conditions as already described for the reduction of fumarate.

Inhibitors.—As shown in Table 5, the rate of uptake of hydrogen in the presence of malate was affected qualitatively by most of the inhibitors in the same manner as the reduction of fumarate.

TABLE 5.

Effect of Inhibitors on the Reduction of Malate.

Each manometer vessel contained $1 \cdot 0$ ml. suspension, about $6 \cdot 5$ mg./ml. dry wt., $1 \cdot 5$ ml. M/5 phosphate buffer pH $6 \cdot 0$. The inhibitor was incubated with the cells during the equilibration period. The side arm contained $0 \cdot 1$ ml. M/1 *dl*-malate. In the centre well was $0 \cdot 2$ ml. 20% KOH.

Inhibitor.					Concentration.	Percentage Inhibition.
Sodium cyanide	..	..	..	..	M/100	40
Do.	..	..	..	..	M/1000	0
Sodium azide	..	..	..	..	M/100	90
Do.	..	..	..	..	M/1000	23
Hydrazine	..	..	..	..	M/50	10
Hydroxylamine	..	..	..	..	M/50	10
Carbon monoxide	..	..	..	$H_2 : CO = 20 : 80$	30
Sodium pyrophosphate	..	..	..	M/50	30
Sodium selenite	..	..	..	..	M/100	0
Sodium fluoride	..	..	..	..	M/50	100
Do.	..	..	..	..	M/100	100
Do.	..	..	..	..	M/300	88
Do.	..	..	..	..	M/600	0
Sodium malonate	..	..	..	..	M/10	35
2 : 4 DNP	..	..	..	..	M/1000	96
m-NP ..	..	..	..	..	M/1000	25
o-NP ..	..	..	..	..	M/1000	+57
p-NP ..	..	..	..	..	M/1000	91
o-Phenanthroline	..	..	..	..	M/500	100
Do.	..	..	..	..	M/3000	92
Sodium iodoacetate	..	..	..	..	M/1000	100
Do.	..	..	..	..	M/5000	75

Outstanding differences with respect to the action of inhibitors on the two systems were noted with sodium azide, sodium fluoride and *o*-phenanthroline. In these cases, the hydrogen uptake in the presence of malate was much more markedly inhibited than was the reaction with fumarate.

Attempts were made to reverse the inhibition by *o*-phenanthroline by addition of ferrous ions, manganous ions, zinc ions and magnesium ions. However, no diminution of the inhibition was obtained under those conditions which reversed to a marked degree, the inhibition by *o*-phenanthroline of the hydrogen-fumarate system.

Preliminary incubation with molecular oxygen inhibited the reduction of *dl*-malate by molecular hydrogen to the same degree as the hydrogen-fumarate system.

The uptake of hydrogen in the presence of *dl*-malate was more sensitive to M/30 maleate and to M/30 succinate than was the uptake in the presence of fumarate.

DISCUSSION.

Studies with inhibitors would seem to suggest that the part of the system activating fumarate rather than that activating the hydrogen was the factor limiting the rate of hydrogen uptake. Thus cyanide, carbon monoxide and hydroxylamine inhibited strongly the reduction of methylene blue by molecular hydrogen but did not inhibit the hydrogen-fumarate or the hydrogen-malate systems to any marked extent. In previous studies on other reactions linked with hydrogen oxidation, similar observations have been made. The QH_2 values when methylene blue was the acceptor were much higher than those observed when either molecular oxygen, nitrate, fumarate or malate were used. It can be assumed that all these acceptors, except methylene blue, required the participation of other enzymes besides hydrogenase.

Hoberman and Rittenberg (1943) have put forward the view that hydrogenase is a ferrous porphyrin enzyme. Of the systems linked with hydrogenase, Granick and Gilder (1945) have produced evidence indicating that the nitratase of *Haemophilus influenzae* may well be an iron porphyrin enzyme. In general, one may say that there is not a great deal known about the enzymes and carriers of all these systems involving the oxidation of molecular hydrogen.

Doubts about permeability invariably introduce difficulties in assessing the value of studies on the enzymes of unicellular organisms. Lynen (1942) has drawn attention to the impermeability of yeast cells to malonate and succinate within the usual pH range. He overcame this difficulty by using a very acid pH. The marked accelerating effect of toluene treatment on the reduction of fumarate by molecular hydrogen in the presence of cells of *E. coli* in this investigation may be due partly to its action on the cell membrane. This is further suggested by the observations on the cell-free extract. The properties of the hydrogen-fumarate system resembled, in this instance, more closely the behaviour of the toluene-treated cells than the normal cells.

The marked difference with respect to the effect of toluene treatment between the hydrogen-fumarate and the hydrogen-malate systems may be due to sensitivity of fumarase to such treatment.

In view of the work of Clifton and Logan (1939), the effect of 2:4 dinitrophenol on the hydrogen-fumarate system was of interest. They found that the rates of oxidation of fumarate and succinate were inhibited markedly by DNP, whereas the rates of oxidation of other substrates tested were affected to a much smaller extent.

In the present investigation, the hydrogen-fumarate system in the extract and in the toluene-treated cells was unaffected by DNP; but, with normal cells, DNP was strongly inhibitory. Sodium azide inhibited the system in the normal cells but to a smaller extent. It exerted no inhibition with the extract or with toluene-treated cells.

Results obtained to date with *o*-phenanthroline do not give any clear indication of its mode of action. Its most pronounced action was on the hydrogen-malate system, which was completely inhibited by M/500 *o*-phenanthroline. This fact, together with the very marked dilution effect on the system, suggested the possibility of a metal component in the enzyme, fumarase. Laki and Laki (1941) have obtained a crystalline fumarase from beef heart, but do not mention the involvement of a metallic ion in this enzyme.

SUMMARY.

The reduction of fumarate and *dl*-malate by molecular hydrogen in the presence of washed suspensions of *E. coli* has been studied.

In general, the properties of the two systems were very similar.

Treatment of the cells with toluene gave a material most suitable for the investigation of the reduction of fumarate. This treatment diminished reduction of fumarate by endogenous hydrogen donators and accelerated the rate of hydrogen uptake in the

presence of fumarate but inhibited strongly the reduction of *dl*-malate by molecular hydrogen.

The inhibitors studied included DNP and *o*-phenanthroline. M/1,000 DNP strongly inhibited the rate of hydrogen uptake in the presence of fumarate by washed cells. This inhibition was not observed with the toluene treated cells. M/500 *o*-phenanthroline inhibited the rate of hydrogen uptake in the presence of fumarate strongly, and completely inhibited the reaction with malate.

A few experiments were carried out with cell-free extracts of the bacteria. In general, the action of inhibitors in these instances closely resembled the behaviour of the toluene-treated cells.

ACKNOWLEDGEMENTS.

BIBLIOGRAPHY.

BACK, K. J. C., LASCELLES, J., and STILL, J. L., 1946.—*Aust. J. Sci.*, 9 : 25.

CLARKEN, O. B., 1938.—*Ann. der Chemie*, 535 : 122.

CLIFTON, C. E., and LOGAN, W. A., 1939.—*J. Bact.*, 37 : 529.

FISCHER, F. G., and EYSENBACH, H., 1937.—*Ann. der Chemie*, 530 : 99.

————, ROEDIG, A., and RAUCH, K., 1939.—*Naturwissenschaften*, 27 : 197.

GAFFRON, H., 1945.—*J. Gen. Physiol.*, 28 : 269.

GRANICK, S., and GILDER, H., 1945.—*Science*, 101 : 540.

HOBERMAN, R., and RITTENBERG, D., 1943.—*J. Biol. Chem.*, 147 : 211.

KALNITSKY, G., UTTER, M. F., and WERKMAN, C. H., 1945 : *J. Bact.*, 49 : 595.

KREBS, H. A., 1937.—*Biochem. J.*, 31 : 2095.

————, SMYTH, D. A., and EVANS, E. A., 1940.—Ibid., 34 : 1041.

LAKI, E., and LAKI, K., 1941.—*Enzymologia*, 9 : 139.   (Seen in Abstract only.)

LASCELLES, J., and STILL, J. L., 1946a.—*Aust. J. Exp. Biol.*, 24 : 37.

————, and ————, 1946b.—Ibid., 24 : 159.

LYNEN, F., 1942.—*Ann. der Chemie*, 552 : 270.   (Seen in Abstract only.)

QUASTEL, J. H., and WHETHAM, M. W., 1924.—*Biochem. J.*, 18 : 519.

SANDELL, E. B., 1944.—Colorimetric Determination of Traces of Metals.   Inter-science Publishers, Inc. New York, N.Y.

STEPHENSON, M., and STICKLAND, L. H., 1931.—*Biochem. J.*, 25 : 205.

WILLIAMSON, S., and GREEN, D. E., 1940.—*J. Biol. Chem.*, 135 : 345.

WOOLF, B., 1929 : *Biochem. J.*, 23 : 478.

NOTES ON AUSTRALIAN MOSQUITOES (DIPTERA, CULICIDAE).

PART VII. THE GENUS HARPAGOMYIA.*

By R. H. WHARTON, B.Sc.

(Twelve Text-figures.)

[Read 30th April, 1947.]

Contents.

INTRODUCTION.

The present paper records for the first time the occurrence of the genus *Harpagomyia* de Meijere in the Australasian Region. *H. genurostris* (Leicester) is recorded from northern Australia and southern New Guinea, one new species is described from northern New Guinea and another from the Solomon Islands. The previous known range of the genus embraced the Ethiopian and Oriental Regions. In the latter region it extended eastwards to the Philippine Islands in the north and to Java in the south.

Although a complete revision of the Oriental species is not at present possible, comparative notes on the Oriental and Australasian species are included in an attempt to facilitate their identification.

Harpagomyia is one of the most remarkable of mosquito genera because of the association of at least some species with ants belonging to the genus *Cremastogaster*. The adults obtain food from these ants by inserting the proboscis between the ants' jaws and absorbing any food offered. This association was first observed by Jacobson (1909a) in Java and was subsequently confirmed by James (1914) in Ceylon, and Farquharson (1918) in Tropical Africa. However, no such relationship has been observed in the Australasian species as, so far, the only adults examined have been bred through from larvae.

Genus HARPAGOMYIA de Meijere.

DE MEIJERE, J. C. H., 1909.—*Tijdschr. Ent.*, 52 : 165.
EDWARDS, F. W., 1921.—*Trans. ent. Soc. Lond.*, 1921 : 496.
————, 1932.—Culicidae in Wytsman's Genera Insectorum. Fasc. 194 : 92.

SYNONYMY.

MALAYA Leicester, 1908 (nec *Malaia* Heller, 1893). Culicidae of Malaya in *Stud. Inst. Fed. Malay States*, 3 : 258. Genotype : *M. genurostris.*
GRAHAMIA Theobald, 1909. Colonial Office Miscell. Publ. No. 237 : 23. Genotype : *G. trichorostris.*

CHARACTERS OF THE GENUS.

Adult.

The most distinctive character of *Harpagomyia* is the proboscis (Text-figs. 1 and 2), which is stout and hairy with a flexible joint at about two-thirds from the base, beyond which it is swollen. On each side of the basal two-thirds is a row of upwardly-directed bristles, and inserted near the base of the labella are four long, curled hairs. Mandibles and maxillae are absent in both sexes.

All species are relatively small, dark coloured mosquitoes with patches of silvery scales on the head, thorax and abdomen. The head is clothed with broad, flat scales, there being a silvery patch on the vertex and similar patches laterally. No upright forked scales are present. The clypeus is elongated and rather pointed, and is in close contact with the proboscis, as are the two-segmented palpi, which are scarcely longer than the clypeus and alike in both sexes. The antennae are alike in both sexes, those of the male lacking distinct plumes.

The prothoracic lobes are well defined and clothed with flat, metallic-silvery scales. Dorsocentral bristles are present on the scutum, which is clothed with narrow, curved scales and often a median line of flat, silvery scales. The scutellar scales are broad and flat. There are one or two posterior pronotal bristles, one to three spiracular, six to ten upper mesepimeral, but no sternopleural, lower mesepimeral or prealar bristles. The pleural scaling is metallic-silvery and extends over the posterior pronota, sternopleura and the upper part of the mesepimera. The postnotum is bare.

The legs are normal, uniformly dark scaled, with simple tarsal claws, those of the front pair in the male being slightly unequal. There are no pulvilli.

The wing scales are moderately broad and pointed, and the wing membrane bears distinct microtrichia. Cu_2* is well developed, almost reaching the wing margin, and the anal vein ends immediately below or a little beyond the junction of Cu_1 and m-cu.

The abdomen is dark brown to black with large silvery spots laterally. The eighth sternite is small and inconspicuous, as are the stout and broad cerci in the female.

Male Terminalia: The coxites, which are scaled ventrally,† are about twice as long as broad and bear ill-defined basal lobes, each with several simple spines. The claspers are curved and simple, with a short, thick terminal spine. The harpagones are simple, bare and pointed, while the phallosome is weakly chitinized, divided or entire.

Larva.

The antennae are short and smooth, with a small, simple shaft hair. The arrangement of the head hairs (Text-fig. 5) is unusual in that hairs A, B and d form a convex row around the anterior margin of the head, with hair C usually much smaller, posterior to B and d, and at or about the level of the bases of the antennae. The mouth parts are unmodified. The clypeal and epicranial sutures are indistinct.

The dorsolateral and ventrolateral thoracic hair tufts are well developed, particularly on the prothorax, where two large fan-shaped tufts arise from a dorsolateral chitinized plate.

The lateral hair tufts on the first two segments of the abdomen are well developed and the individual hairs rather long. The tufts on the following segments consist of fewer and finer hairs, though the individual hairs are still long. On the siphon there is one pair of true ventrolateral hair tufts distal to which is an irregular row of unpaired smaller tufts extending to the apex of the siphon. Dorsolateral hair tufts are present, variable in number and relative position. There is no acus and the pecten is extremely variable. The saddle, from which arises a very long saddle hair, is weakly chitinized and bears laterally a patch of relatively large scales. The ventral brush is reduced to two or three fine hairs which may be single or branched.

* In conformity with the terminology proposed by Lee and Woodhill (1944, p. 22). Other authors either do not name, or merely refer to, this vein as an accessory vein or thickening.
† Edwards (1941) states that the coxite bears "scales on its dorsal surface", but the scales are on the ventral surface before the tip of the abdomen rotates.

RELATION TO OTHER GENERA.

The genus *Harpagomyia* resembles the Oriental genus *Topomyia** (Theobald) in many details, and apart from the modified mouth parts in *Harpagomyia*, there is little to separate the adults of the two. When larval characters are examined it is found that no constant differences between the two genera can as yet be established. Within the Australasian Region the only genus with which the larva could be confused is the genus *Tripteroides* Giles. In both genera the ventral brush is much reduced, but *Harpagomyia* differs in the complete absence of stellate hair tufts, large spines on the thorax, or any modification of the maxillae.

AUSTRALASIAN SPECIES.

HARPAGOMYIA LEEI, n. sp.

Types: Holotype female, allotype male, and two female paratypes deposited in the Museum of the Division of Economic Entomology, Council for Scientific and Industrial Research, Canberra, A.C.T., and two female paratypes in the Macleay Museum, University of Sydney.

Type Locality: Madang, New Guinea. (M. M. H. Wallace, January, 1946.)

DESCRIPTION.

Female.

Head: The head is clothed with broad, flat scales—a large triangular patch of silvery scales on the vertex continued anteriorly for a short distance between the eyes, a patch of similar scales laterally on either side, and the remainder of the head covered with dark-brown to black scales. The antennae are slightly longer than the proboscis, the pedicels and flagella dark brown, the former with a greyish sheen. The first flagellar segment is longer than the remaining segments which are all about equal, with dark brown clothing and verticillate hairs. The clypeus is elongated, only slightly shorter than the palpi, both clypeus and palpi being light brown with silvery-grey sheen. The basal two-thirds of the proboscis is light brown, darker underneath than on top, with scattered spatulate creamy scales, light brown clothing hairs, and a row of upwardly-directed, dark brown, long hairs on each side. The apical third is dark brown with dark brown to black flat scales and hairs.

Thorax: The integument is dark, reddish-brown, the mesonotum being uniformly covered with narrow-curved, light brown scales except for a median, longitudinal line of flat, white, silvery scales extending from the front margin to about the level of the wing roots. There are further patches of flat, white, silvery scales on the prothoracic lobes, a small patch on the propleuron, a very large continuous covering to the sternopleuron and upper mesepimeron, and a large patch on the middle lobe and inner margins of each lateral lobe of the scutellum. The large, almost circular, flat scales on the proepimeron appear quite black in some lights but in others show metallic, golden-brown reflections. The outer edges of the lateral lobes of the scutellum are clothed with broad, flat, dark brown to black scales. The postnotum is brown and bare, the stems of the halteres are light brown, the knobs being covered with dark brown flat scales.

Legs: On the anterior surface of the fore coxae and lateral surfaces of the mid and hind coxae there is a patch of silvery, flat scales. The rest of the legs are entirely dark scaled except for the undersurface of the femora and to some extent the tibiae. The tibiae of all legs, particularly those of the hind legs (Text-fig. 3), are enlarged apically, and in the latter, the first tarsal segment is distinctly longer than the tibia.

Wings (Text-fig. 12): The wings are entirely clothed with dark brown scales which are rather broader and more numerous on the basal sections of the costa, subcosta and radius. The upper fork cell is 2·3 times as long as its stem, with its base nearer the base of the wing than that of the lower fork cell, which is approximately equal in length to its stem. The posterior cross-vein is its own length from the anterior cross-vein.

---

* The genus *Topomyia* has been recorded by Brug (1939) as far east as the Celebes, breeding in leaf axils of *Colocasia*, but has not yet been found in the Australasian Region.
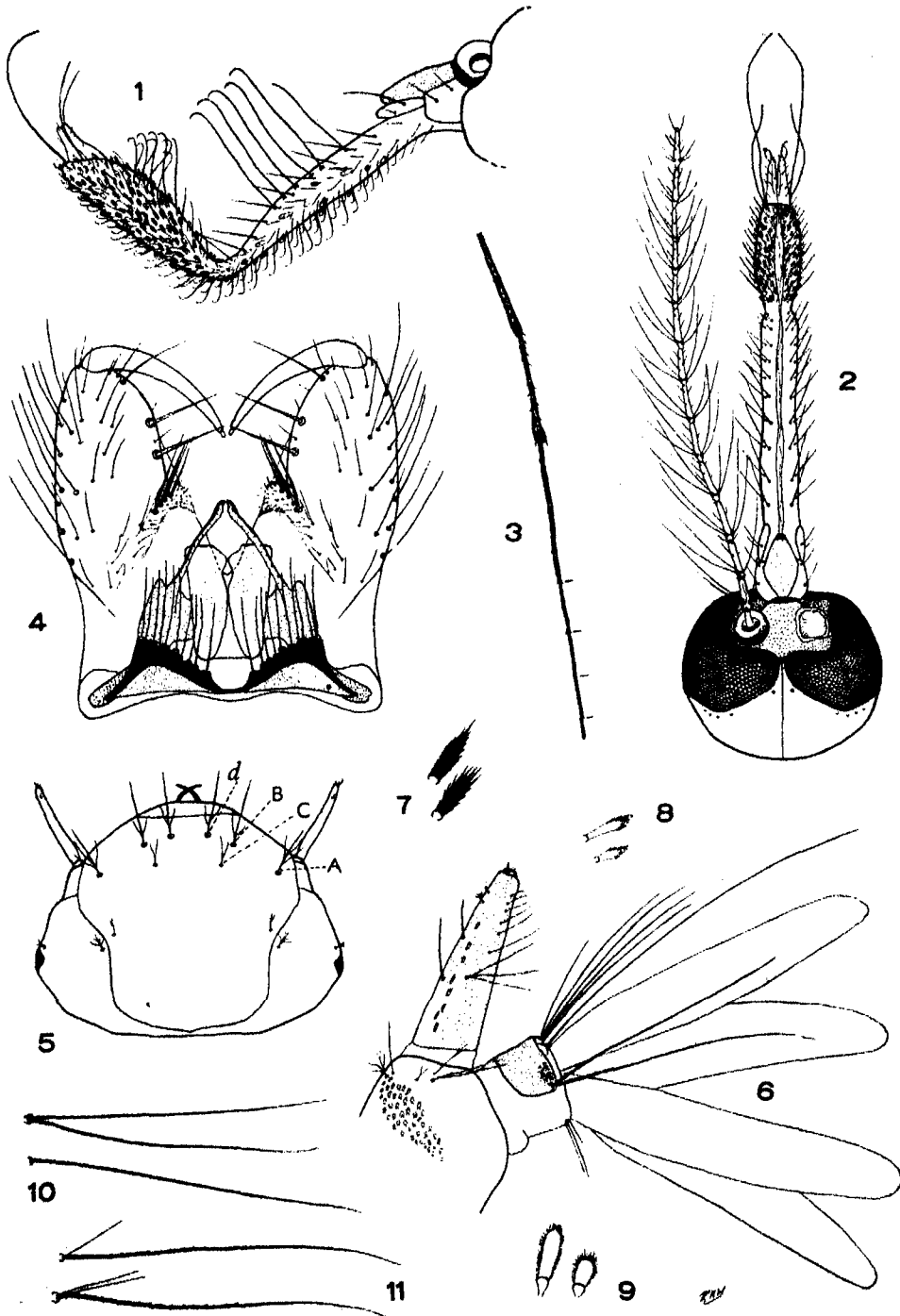
Text-figs. 1-10.—*Harpagomyia leei*, n. sp.

1. Proboscis, palpus and clypeus, lateral view, × 70 approx. 2. Head, dorsal view, × 50.
3. Hind leg, × 15. 4. Genitalia, × 200. 5. Head of larva, × 200. 6. Terminal segments of larva,
× 50. 7. Pecten teeth, × 200. 8. Saddle scales, × 200. 9. Lateral comb scales, × 200.
10. Variations in saddle hair, × 54.

Text-fig. 11.—Variations in saddle hair of *H. genurostris*, × 54.

Abdomen: The abdomen has a complete covering of broad, overlapping, flat scales. Apart from large triangular silvery-white patches apically on the lateral margins of segments I, II, IV and V, and a minute patch on segment VI, the scales on the tergites are all dark.

Male.

Essentially the male is similar to the female except that the large, flat scales on the posterior pronotum show more brilliant reflections than in the female, though still not as brilliant as is found on the metallic scaling elsewhere.

Genitalia (Text-fig. 4): The lobes of the ninth tergites are strongly chitinized and have nine or ten spines on each lobe. The basal lobes of the coxites are small and bear four strong bristles, above which, on the inner surface of each coxite, are two similar bristles. The phallosome is partly divided, with small projections on the apex.

Larva.

The larva of *H. leei* is rather inconspicuous when alive because of the general light brown colouration.

Head (Text-fig. 5): The clypeal spines are rather long and moderately stout; head hairs A, B and d are approximately equal in size, C is much shorter and finer; A has three to five branches and occasionally six; B is normally trifid, but may be bifid; d has from three to five branches; C is normally bifid but may be single or trifid; e has about three fine branches, and f is weak, with five or six branches.

Terminal Segments (Text-figs. 6–9): The lateral comb consists of from thirty to sixty fringed scales arranged in a large subtriangular patch. The pentad hairs are weak and located more towards the siphon than is usual; the first pentad hair has six or seven finely frayed branches; the second is single and similarly frayed; the third is small and smooth and has from one to four branches; the fourth is frayed and has from one to three branches; and the fifth has normally two, but occasionally three, frayed branches. The siphon is weakly chitinized, particularly towards the base, and the siphonal index is about 3. The ventrolateral hair tuft has three or four slightly plumose branches, the following row of tufts consists of from two to four single, frayed hairs, followed by one or two smooth hairs with two to four branches. The dorsolateral hair tufts consist of from two to four normally single, occasionally bifid, frayed hairs followed by one to three smooth, smaller hairs with six or seven branches on the apex of the siphon. The pecten is extremely variable; in some specimens it is composed of an irregular group of small transparent fringed teeth near the base followed by a widely spaced row of four or five larger fringed teeth. In other specimens the pecten is reduced to three or four fringed teeth which form an irregular row on the siphon, and all types of gradation between these two extremes have been seen. The saddle normally covers between one-half and two-thirds of the anal segment, the saddle hair (Text-fig. 10) is very long, pilose at its base, and usually with two approximately equal branches, but sometimes it is single.
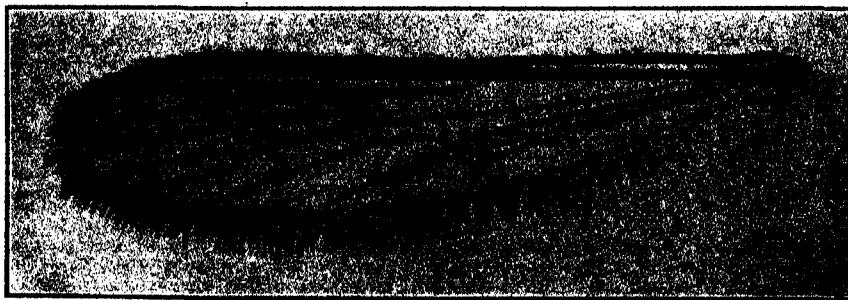
Text-fig. 12.—*Harpagomyia leei*, n. sp. Wing of female, x 43.

The dorsal subcaudal hair tuft has four or five branches, and the ventral subcaudal tuft is single. The ventral brush is reduced to two fine hairs and in one specimen an additional small hair is present. The anal papillae are extremely large, moderately wide and at least three times the length of the anal segment.

Breeding Habitat: Leaf axils of *Colocasia* sp.

Distribution: Madang, New Guinea.

Note.—Lieut.-Col. W. V. King obtained larvae of an undetermined species of *Harpagomyia* from the leaf axils of taro plants, *Colocasia* sp., in the Dobodura–Cape Sudest area, New Guinea, in 1943. His brief description of the adults reared from these larvae (in "Keys to the Culicine Mosquitoes of the New Guinea Region", a roneoed document prepared for the U.S. Army, Third Medical Laboratory, October, 1944) indicates that they may have been *H. leei*, but the specimens were not available for examination.

HARPAGOMYIA SOLOMONIS, n. sp.

Types: Holotype male, allotype female, one male paratype in the University of Queensland Collection. Holotype and allotype with associated larval and pupal skins.

Type Locality: Bougainville (J. R. Covell, December, 1944).

DISTINCTIVE CHARACTERS.

H. solomonis, although closely related to *H. leei*, is distinct in both the male and the larva. In the adult male the scutellum has broad, flat, dark brown scales on all lobes, but no silver scales on the mid-lobe as in *H. leei*. The larva differs in head hair C being much longer and stouter, almost as well developed as A, B and d. The saddle hair consists of three or four equal branches and the hairs of the ventral brush are almost as long as the saddle hair.

DESCRIPTION.

Male.

Head: The scales of the head are broad and flat, the silver patch on the vertex not continued anteriorly between the eyes. The pedicels and first flagellar segments are light brown with a greyish sheen. The base of the proboscis, palpi and clypeus are cream, the remainder of the basal two-thirds of the proboscis light brown with scattered cream scales on the upper surface and darker brown scales underneath.

Thorax: The integument is reddish-brown, the mesonotum with narrow, curved, dark brown scales and a median line of flat, almost circular, silver scales. Pronotal lobes are silver scaled and proepimeral scales appear dark brown, bronze or silver according to the direction of light. At most only two fine spiracular bristles are present. The scales on all three lobes of the scutellum are flat and dark brown in colour.

Legs: The coxae are very light brown, each with a patch of silvery, flat scales, the remainder of the legs uniformly dark scaled.

Wings: The scales on the wing and the position of the fork cells are as in *H. leei* (Text-fig. 12).

Abdomen: The dorsum is entirely dark scaled, the anterior, lateral margins of tergites I, II, IV and V with patches of silver scales. Tergites VI, VII and VIII are completely dark scaled.

Genitalia: The genitalia are similar to those figured for *H. leei* but the harpagones are less pointed and have much stouter stems.

Female.

The clypeus, except for the tip, is dark brown in colour, the palpi and basal two-thirds of the proboscis slightly darker than in the male.

The scutellum, though partly denuded, bears a number of broad, flat silver scales on the mid-lobe and dark brown, flat scales on the lateral lobes.

The legs, wings and abdomen agree in all essentials with those of the male.

Larva.

Head: Head hairs A, B, C and d are approximately equal in length; A has six branches; B has from three to five branches; C has two or three branches and d has

five or six branches. Head hair C normally has only one branch which is approximately equal in length to the longest branches of hairs A, B and d, the remaining branches of C being much shorter.

Terminal Segments: The ventrolateral hair tuft on the siphon has about five finely frayed branches; the row of hairs on the ventral surface consists of eight or nine single or bifid finely frayed hairs. The pecten is variable.

The saddle is well developed and covers the upper two-thirds of the anal segment; saddle hair very long with three or four pilose branches which are approximately equal in length. The dorsal subcaudal hair tuft has four to six branches, all simple, while the ventral subcaudal tuft is an extremely long single hair. The ventral brush consists of two long, single, or bifid hairs about the same length as the saddle hair.

Breeding Habitat: According to J. R. Covell, larvae were found "breeding in axils of a lily-like plant with long narrow leaves, grows 3–7 feet high". A botanist reported on specimens, "That as far as can be ascertained, its family is Pandanaceae and genus *Sararanga*."

Distribution: Bougainville Island.

Note.—The colour of the clypeus in the female is distinctive but may not be a constant character and could only be verified by the examination of further specimens.

The description of the larva was made from correlated larval skins which were, unfortunately, poor preparations. No larval material was available and further collections are required before a fuller description and figures can be attempted.

<h2 style="text-align:center">HARPAGOMYIA GENUROSTRIS (Leicester).</h2>

LEICESTER, G. F., 1908.—Culicidae of Malaya in *Stud. Inst. Med. Res. Fed. Malay States*, 3 : 258.
EDWARDS, F. W., 1913.—*Bull. ent. Res.*, 4 : 230.
————, 1921.—*Trans. ent. Soc. Lond.*, 1921 : 498.
————, 1930.—*Bull. ent. Res.*, 21 : 543.
BARRAUD, P. J., 1926.—*Ind. J. Med. Res.*, 14 : 349.
————, 1934.—Fauna Brit. Ind., Dipt., 5 : 48.
BOHART, R. M., and INGRAM, R. L., 1946.—Navmed 1055. Bur. Med. and Surgery, Navy Dept., Wash. : 54.

Types: Type male in the British Museum.

Type Locality: Kuala Lumpur, Malay Peninsula.

Material Examined: I have examined a series of specimens collected from Darwin and Cairns (Australia), and Merauke (Dutch New Guinea).

<h3 style="text-align:center">DISTINCTIVE FEATURES.</h3>

The adult may be distinguished by the cream to light brown colour of the basal two-thirds of the proboscis, clypeus and palpi, by the presence of a line of silver scales between the eyes, and the presence of large apical lateral patches of silver scales on tergites VI and VII.

Larval differences are discussed in the description below.

<h3 style="text-align:center">DESCRIPTION.</h3>

Female.

The basal two-thirds of the proboscis, the clypeus and palpi vary from yellow to light brown, the apical third dark with a complete covering of dark brown to black scales. The patch of silver scales on the vertex is continued anteriorly as a narrow silver line between the eyes.

The integument of the mesonotum ranges from light to dark reddish-brown and the median line of metallic scales may appear silver or bluish according to the angle and intensity of the illuminating light. The silvery metallic scales on the prothoracic lobes and proepimera can also vary, the former from pearly-white to azure-blue, the latter from white to yellow, but the reflections from these are never as brilliant as those from the prothoracic scales.

There are large apical patches of silver scales on the lateral margins of all the abdominal tergites except the third, the patches on tergites IV and VII being the largest and almost covering the sides of the tergites.

Male.

Only the tip of the apical third of the proboscis is definitely dark, the remainder cream to light brown. The original description, based on a single male, states that the scutellar scales are "small, dark brown, and racquet-shaped". Specimens from Darwin have broad, flat, dark brown scales on all lobes, but specimens from Cairns have flat, silver scales on the mid-lobe and flat brown scales on the lateral lobes as in the female. The Merauke material is badly rubbed and the only specimen with any scaling has two broad, flat, dark brown scales on the apex of the mid-lobe and scattered similar scales at the base of all lobes. Neither Barraud (1926, 1934) nor Edwards (1913, 1922, and 1930) deals clearly with the scutellum, though Barraud (1926) mentions that the "scutellar scales are silvery", but he does not disclose any sexual differences. In the type male, according to information received from the British Museum, the scutellum is denuded and the examination of further specimens points to the conclusion that the scaling of the scutellum in male *H. genurostris* is a variable character.

The male is similar to the female in all other essential details, and the genitalia show no marked differences from those figured for *H. leei*.

Larva.

The larva has been figured by Barraud (1934, Fig. 12, g–j) and is very similar to *H. leei*. The only points of difference may be in the dorsolateral hair tufts on the siphon, which are smaller and have two or three smooth branches instead of the frayed, normally single, hair tufts in *H. leei*. Again, the saddle hair (Text-fig. 11) consists of one very long branch and one, in rare cases two, much finer and shorter branches. However, *Harpagomyia* larvae are, as a group, extremely variable, and it is likely that the above characters would break down if a larger series of larvae from both species were examined.

Breeding Habitat: The larvae have been found breeding in the leaf axils of large *Arum* (Barraud, 1934), in cunjevoi, probably taro (Wassell, 1944), in *Colocasia* (Wharton, 1945), and in *Colocasia antiquorum* and *Rhynchospora aurea* (Cyperaceae) (Marks, 1946).

Distribution: Previously known in India, Ceylon, Assam, Malaya, Philippines, Ryukyus, Okinawa and possibly Formosa. New Guinea (Cameron, 1945), Australia, Cairns (Wassell, 1944, and Marks, 1946) and Darwin (Wharton, 1945) are new records.

Credit for the first discovery of *H. genurostris* in Australia belongs to J. C. Wassell, who collected larvae at Cairns in June, 1944.

The presence of *H. genurostris* in Java and Sumatra has been recorded by several authors, but the evidence on which this is based is not known to me. Edwards (1921), in a revision of the genus, reduced the number of Oriental species to one, namely, *H. genurostris*, which was then regarded as having a distribution which included Java and Sumatra. In a subsequent paper (1930), Edwards restored the original species, and by virtue of this restoration and the absence of new records, the distribution of *H. genurostris* at present appears to exclude Java and Sumatra.

ORIENTAL SPECIES.

Harpagomyia genurostris was originally described from Malaya in the Oriental Region but its distribution now includes parts of the Australasian Region. The distinctive features of *H. genurostris* have been set out above, notes on the remaining Oriental species follow.

HARPAGOMYIA COERULEOVITTATA Ludlow.

LUDLOW, C. S., 1911.—*Psyche*, 18 : 131.
EDWARDS, F. W., 1913.—*Bull. ent. Res.*, 4 : 240.
————, 1930.—Ibid., 21 : 543.

Types: Type female in the United States National Museum, Washington.
Type Locality: Philippine Islands.
Material Examined: No specimens were available for examination, but Lieut.-Col. W. V. King, of the United States Army, kindly examined the type female and forwarded a description.

DESCRIPTION.

Because Ludlow described the clypeus as having a "rather long, white fuzzy tomentum", Edwards (1930) regards this species as distinct. Lieut.-Col. King formed

the opinion that there is definitely no tomentum, but that the clypeus is "shiny dark brown, appearing frosted in some lights". King further mentioned that the specimen has apparently darkened in colour, and, as the remainder of the description follows that for *H. genurostris* it appears likely that *H. coeruleovittata* is a synonym of *H. genurostris*.

The larva has not been described.

Distribution: Philippine Islands.

HARPAGOMYIA JACOBSONI Edwards.

EDWARDS, F. W., 1930.—*Bull. ent. Res.*, 21 : 543.
BARRAUD, P. J., 1934.—Fauna Brit. Ind., Dipt., 5 : 51.
    Types: Type female in the British Museum.
    Type Locality: Fort de Kock, Sumatra.

DESCRIPTION.

Adult.

Apart from being larger than the other described species (wing length 3–3·5 mm. to *H. genurostris* 2·2–2·4 mm.), *H. jacobsoni* is apparently distinct in having a dark clypeus with a slight silvery pruinescence, and in the absence of silver scales between the eyes. The abdominal scaling is similar to *H. genurostris*.

Larva.

The larva has been figured by Barraud (1934, Fig. 12, c–f) and the most obvious differential characters are the unbranched head hairs, the lateral comb composed of from 16–20 teeth more or less arranged in two rows, the anal papillae more pointed than rounded, and the three fairly long branches to each of two hair tufts of the ventral brush.

Breeding Habitat: Leaf axils of a large species of *Arum*, in association with *H. genurostris* (Barraud, 1934).

    Distribution: India, Sumatra.

HARPAGOMYIA SPLENDENS de Meijere.

DE MEIJERE, J. C. H., 1909.—*Tijdschr. Ent.*, 52 : 167.
EDWARDS, F. W., 1930.—*Bull. ent. Res.*, 21 : 543.
    Types: If designated as such, presumably in the "Museum der Kgl. Zoolog. Gesellschaft Natura Artis Magistra", in Amsterdam.
    Type Locality: Java (listed localities are Batavia and Semarang).
    Material Examined: I have examined a series of adults collected by D. H. Colless from Labuan Island, Borneo, another series collected by R. L. Lehfeldt from the same source, and two specimens from Weltevreden, Java. Larval material from Labuan Island was available for examination.

DESCRIPTION.

Adult.

The characters which serve to distinguish this species are as follows: (i). In the female the basal two-thirds of the proboscis is dark brown to black, the clypeus is cream to light brown with a silvery-grey pruinescence. The thorax and abdomen are darker than in *H. genurostris* but the ornamentation is similar. (ii). In the male the basal two-thirds of the proboscis, clypeus and palpi are cream to light brown and the scutellum has a covering of silver, flat scales on the mid-lobe. The male, then, cannot be distinguished superficially from some male *H. genurostris* specimens, and there are no obvious differences in the genitalia.

Larva.

The larva cannot be separated from that of *H. genurostris*. Those examined differ from de Meijere's original description in that the lateral comb is composed of from fifty to sixty scales instead of thirty, and the anal papillae are at least twice as long as, instead of being shorter than, the anal segment.

Breeding Habitat: Larvae were found breeding in the leaf axils of *Colocasia* sp. on Labuan Island.

    Distribution: Java and Borneo (Labuan Island).

BY M. H. WHARTON. 67

Note.—It is possible that the specimens examined from Labuan Island are not true
H. splendens but actually a variety of *H. genurostris* in which the basal portion of the
proboscis is darker than usual. It does appear to be an intermediate form and some
specimens cannot be definitely included in either species, provided, of course, that
H. splendens is a valid species. The present known distribution of *H. genurostris*
supports the above theory in that the presence of *H. genurostris* in the Netherlands
East Indies has not been recorded, though it occurs both east and west of those islands.

One female specimen collected by C. Cameron from Merauke, New Guinea, in 1945,
is very close to *H. splendens*. The proboscis is dark brown to black in colour, but the
clypeus appears to be dark brown with a greyish pruinescence. Further collections
from that area will possibly throw light on the complexity of the *H. genurostris* and
H. splendens problem.

KEYS TO AUSTRALASIAN AND ORIENTAL SPECIES OF HARPAGOMYIA.

When an attempt is made to separate the five, possibly six, species of *Harpagomyia*
which occur in the Australasian and Oriental Regions, considerable difficulties are
encountered.

The examination of the individual species descriptions shows apparent clear-cut and
obvious differences. Each species, however, shows considerable variation, particularly
in the larval stage, and intermediate forms are not uncommon when two closely related
species are studied. It appears that though the genus is extremely specialized, a
number of new species or subspecies are in the process of evolution but have not been
isolated for a sufficient period to have reached a static and constant form. By systematic
and exhaustive collecting over the whole area an interesting problem in geographic
isolation could possibly be elucidated or the number of species curtailed.

(*a*). ADULTS.

1. Basal two-thirds of proboscis and clypeus yellow, cream or light brown 2
   Basal two-thirds of proboscis and clypeus either yellow to light brown or dark brown
        to black but never with basal half of proboscis and clypeus both yellowish in the
        same specimen 3
2. Abdomen with apical silvery patches on all tergites except the third; eyes separated
        completely by a line of silver scales .... *genurostris*
   Abdomen with apical silvery patches on all tergites except the third and seventh,
        and only a small silver spot apically on the sixth; eyes separated for only a short
        distance by a projection anteriorly from the patch of silver scales on the
        vertex .... *leei*
3. Basal two-thirds of proboscis dark brown to black; clypeus yellowish .... *splendens*
   Basal two-thirds of proboscis yellowish; clypeus dark brown to black 4
4. Tergites VI and VII completely dark scaled .... *solomonis*
   Tergites VI and VII with patches of silver scales apically .... *jacobsoni*

The above key should be sufficient to determine female specimens of *Harpagomyia*
and, except in the case of *H. splendens* and *H. solomonis*, will serve to distinguish
males. Since the validity of the specific status of *H. coeruleovittata* is in question, it
has not been included.

(*b*). LARVAE.

1. Lateral comb composed of 16–20 scales arranged in two irregular rows; head hairs
        A, B and d all single .... *jacobsoni*
   Lateral comb a patch of thirty or more scales; head hairs A, B and d always
        branched 2
2. Saddle hair with one long branch, and one, occasionally two, much finer and
        shorter .... *splendens, genurostris*
   Saddle hair single, or, if branched, with all branches approximately equal in size
        and length 3

3. Saddle hair single or with two equal branches .... *leei*

Saddle hair with three or four equal branches .... *solomonis*

ACKNOWLEDGEMENTS.

For helpful criticism and advice I particularly desire to thank Mr. D. J. Lee, of the University of Sydney. Miss E. N. Marks, of the Queensland University, has been of great assistance in providing material and suggestions. Lieut.-Col. W. V. King, of the United States Army, and Mr. H. Oldroyd, of the British Museum, assisted by examining type specimens lodged overseas; and my, thanks are due to Miss G. Burns, of the Department of Zoology, University of Sydney, for the photograph.

REFERENCES.

BOHART, R. M., and INGRAM, R. L., 1946.—Mosquitoes of Okinawa and Islands in the Central Pacific. Navmed 1055, Bur. Med. and Surgery, Navy Dept., Wash.: 54.

BRUG, S. L., 1939.—Notes on Dutch East Indian Mosquitoes. *Tijdschr. Ent.*, 82 : 96-99.

EDWARDS, F. W., 1941.—Mosquitoes of the Ethiopian Region. Part iii. Brit. Mus. (Nat. Hist.), Lond.: 33-37.

FARQUHARSON, C. O., 1918.—*Harpagomyia* and other Diptera fed by *Cremastogaster* Ants in S. Nigeria. *Proc. ent. Soc. Lond.*, 1918 : xxix-xxxix. (Letter communicated by Professor Poulton.)

HOPKINS, G. H., 1936.—Mosquitoes of the Ethiopian Region, Part i. Brit. Mus. (Nat. Hist.), Lond.: 34-36.

JACOBSON, E., 1909a.—*Notes Leyden Mus.*, 31 : 246.

————, 1909b.—Ein Moskito als Gast. *Tijdschr. Ent.*, 52 : 158-164.

————, 1911.—Nähere Mitteilungen über die myrmecophilen Culicide *Harpagomyia splendens* de Meijere. Ibid., 54 : 158-161.

JAMES, S. P., 1914.—Summary of a Year's Mosquito Work in Ceylon. *Ind. J. Med. Res.*, 2 : 233.

LEE, D. J., and WOODHILL, A. R., 1944.—The Anopheline Mosquitoes of the Australasian Region. Univ. Sydney, Dept. Zool., Monogr. No. 2.

DE MEIJERE, J. C. H., 1911.—Zur Metamorphose der myrmecophilen Culicide *Harpagomyia splendens* de Mejeire. *Tijdschr. Ent.*, 54 : 162-67.

THEOBALD, F. V., 1910.—Monograph of Culicidae, 5 : 547.

REPTILES OCCURRING ABOVE THE WINTER SNOWLINE AT MT. KOSCIUSKO.

By Stephen J. Copland, B.Sc.

[Read 30th April, 1947.]

I. Introduction.

This paper was suggested by Dulhunty's observations (1947, pp. 292–295) on sub-snow temperatures at Mt. Kosciusko, and my short note which he kindly published with his work is included and expanded here.

Dulhunty placed thermometers at different depths in a peat bed and allowed them to remain throughout the winter of 1945 to determine the minimum temperatures reached at different levels. Results indicated that sub-surface winter temperatures do not fall below 32°F. even at a depth of nine inches below the surface, although atmospheric temperature at times approaches zero in autumn before the ground is covered with snow and an equilibrium temperature of 32°F. is maintained on the surface beneath winter snow for about eight months of the year.

These observations are of particular interest from the standpoint of low temperature tolerance and conditions of hibernation in reptiles. In this note I have restricted attention to the six species of lizards and two of snakes—listed below—which are non-migratory and undoubtedly live the year round on the high plateau country between the height of the Hotel Kosciusko (5,000 feet) and the summit of Mt. Kosciusko (7,308 feet).

All the reptiles are small (except *Denisonia superba*, and even this snake is much larger at lower altitudes) to avail themselves of the advantageous surface-mass ratio in absorbing heat.

There is little doubt that there will be additional records for the reptilian fauna of the Mt. Kosciusko high plateau country, but the present list may serve as a basis for future work.

II. List of Reptiles.

Amphibolurus diemensis (Gray).

1 (Author's Collection 1600) 1 m. west of the Hotel Kosciusko, 24.i.1943.

This lizard was caught while sunning itself on top of a granite boulder. Three specimens are recorded without definite altitudes from Mt. Kosciusko by Loveridge (1934, p. 323); one (Museum of Comparative Zoölogy 32965) "taken December 10–14, 1931, only 130 mm. in total length, holds eggs measuring 14 × 9 mm."

Tiliqua casuarinae casuarinae (Duméril and Bibron).

1 (Museum of Comparative Zoölogy 33250) Daner's Gap, at 5,400 ft. on Mt. Kosciusko (R. J. Tillyard), 1931. "The Skink was taken in a nest of *Myrmecia pilosula*." Loveridge (1934, p. 365). Malcolm Smith (1937, p. 233) referred the genus *Omolepida*, to which this lizard was formerly attributed, to *Tiliqua*.

Egernia whitii whitii (Lacépède).

2 (A.C. 1547–8) near Chalet, 21.i.1943.

1 (A.C. 1579) 1·2 m. from Hotel Kosciusko towards summit, 23.i.1943.

This lizard is rather uncommon at higher altitudes in contrast to its remarkable numbers near the base of the mountains.

SPHENOMORPHUS QUOYII TYMPANUM (Lönnberg and Andersson).

4 (R 4654 etc., Aust. Mus.) Mt. Kosciusko, 3,000–7,000 ft., holotype and paratypes of *Lygosoma (Hinulia) quoyii kosciuskoi* Kinghorn. Kinghorn (1932, p. 359).

10 (M.C.Z. 33301–10) Mt. Kosciusko (Harvard Exped.) 1931. "Taken in Diggers Creek at about 5,000 ft. . . . Near the water, sometimes on rocks jutting into the stream. Occasionally takes to the water when pursued. (W.E.S.)." Loveridge (1934, p. 350).

1 (A.C. 1545) 2 m. from summit of Mt. Kosciusko, 21.i.1943.

1 (A.C. 1552) 3 m. from Betts Camp towards Hotel Kosciusko, 21.i.1943.

7 (A.C. 1559–65) 4 m. from hotel towards summit, 22.i.1943.

1 (A.C. 1580) 1·2 m. from hotel towards summit, 23·i.1943.

12 (A.C. 1583–8, 1602–7) near hotel, 23–24.i.1943.

The skink collected at the highest altitude, No. 1545, was running in wet grass in a small stream carrying melting ice and snow into the Snowy River. Many lizards were seen sunning themselves on logs, timber, pipes and stones beside Diggers Creek, near the Hotel Kosciusko, or hunting in wet grass beside the stream. They took to the water without hesitation, swimming with a quick paddling motion almost as if running on the surface. They invariably returned to the place from which they had been disturbed, often within a minute. *Sphenomorphus quoyii tympanum* is second only to *Leiolopisma entrecasteauxii* in abundance.

LEIOLOPISMA ENTRECASTEAUXII (Duméril and Bibron).

2 (M.C.Z. 33216–7) Mt. Kosciusko at 6,500 ft. (W. E. Schevill), 1931. Loveridge (1934, p. 358).

14 (M.C.Z. 33218–32) Mt. Kosciusko at 5,400–6,000 ft. (Harvard Exped.), 1931. Loveridge (1934, p. 358).

13 (A.C. 1530–42) near summit of Mt. Kosciusko, about 7,300 ft., 20.i.1943.

1 (A.C. 1546) 3 m. from summit, near road, 21.i.1943.

1 (A.C. 1549) near Chalet, 21.i.1943.

1 (A.C. 1551) 3 m. from Betts Camp towards Hotel Kosciusko, 21.i.1943.

6 (A.C. 1553–8) 4 m. from hotel towards summit, 22.i.1943.

1 (A.C. 1568) 2·5 m. from hotel towards summit, 22.i.1943.

9 (A.C. 1569–71, 1573–8) 1·2 m. from hotel towards summit, 22–23.i.1943.

4 (A.C. 1589–91, 1601) near hotel, 23–24.i.1943.

2 (A.C. 1598–9) 1·6 m. from hotel towards summit, 24.i.1943.

Nos. 1530–42 were collected in half an hour within 50 yards of the summit on a cold but sunny afternoon. All were active although they were resting under rocks in grass and low, thick vegetation. Snow and ice were lying in patches over the grass and rock, forming tongues between the clear areas. The remaining lizards were found in rather similar circumstances or foraging actively in the grass. Many escaped in cracks and joints of granitic rocks. *Leiolopisma entrecasteauxii* is undoubtedly the most common reptile over 5,000 feet.

HEMIERGIS DECRESIENSIS TALBINGOENSIS Copland.

3 (R 530, R 522–3, Aust. Mus.) Mt. Kosciusko, 5,000 ft. (R. Helms) v. 1889.

I made an unsuccessful search for this lizard. The three specimens referred to here are discussed by Copland (1946, p. 77 *et al.*).

DENISONIA SUPERBA (Günther).

1 (A.C. 1567) 4 m. from Hotel Kosciusko towards summit, 22.i.1943.

1 (A.C. 1581) 1·2 m. from hotel towards summit, 23.i.1943.

1 (A.C. 1593) near hotel, 23.i.1943.

Nos. 1567 and 1581 were found under large stones on wet, grassy hillsides. No. 1593 was first seen gliding through grass between Diggers Creek and the Hotel Kosciusko. When cornered, it flattened its neck to a surprising extent. The snake is known locally as the "Yellow-bellied Black Snake". Loveridge (1934, p. 284) records two specimens,

the larger 798 mm., collected on Mt. Kosciusko by W. E. Schevill in 1931, but does not give the altitude.

DENISONIA CORONOIDES (Günther).

4 (M.C.Z. 32815–8) below Dead Horse Pass, near the summit of Mt. Kosciusko (P. J. Darlington), 1931. Loveridge (1934, p. 285).

1 (A.C. 1550) 3 m. from Betts Camp towards Hotel Kosciusko, 21.i.1943.

1 (A.C. 1566) 4 m. from hotel towards summit, 22.i.1943.

1 (A.C. 1572) 1·2 m. from hotel towards summit, 22.i.1943.

1 (A.C. 1582) as preceding, 23.i.1943.

1 (A.C. 1592) near hotel, 23.i.1943.

Snakes collected on 21st and 22nd January were sluggish when uncovered and for some time made no attempt to escape. On the warmer 23rd January, No. 1582, which was found gliding through grass, was very active, and No. 1592 was sunning itself on a grassy hillside. This pretty little snake is very common. No two specimens agreed in ventral colour; different specimens were dark orange, salmon-pink, dirty white with posterior half of tail pale pink, yellowish-grey bordered by red, and yellowish becoming orange caudad, respectively.

I have collected *Tiliqua nigrolutea* Gray, *Leiolopisma trilineata* (Gray) also noted by Loveridge from Mt. Kosciusko (1934, p. 359), *L. weekesae* Kinghorn, and *L. guichenoti* (Duméril and Bibron) at elevations somewhat below 5,000 feet and believe it unlikely that they extend above this height. *Amphibolurus muricatus* (Shaw) is noted without definite elevation from Mt. Kosciusko by Loveridge (1934, p. 323).

III. DISCUSSION.

Less work appears to have been done on the behaviour of reptiles at low temperatures with associated problems of hibernation and survival than at critical thermal levels.

Conditions at Mt. Kosciusko must be somewhat similar to those reported by Stebbins (1944, pp. 233–245) in part of Lassen Volcanic National Park, California. Stebbins says: "The season of activity for the mountain swift at this elevation (6,000 feet) is quite short . . . estimated tentatively to be between five and six months . . . during the winter the area may be covered with from two to four feet of snow, exclusive of drifts."

Cowles (1941), in a study of Californian desert reptiles in winter, says (p. 139): "A study of the hibernation preferences of 96 specimens of 14 species shows that most prefer shallow retreats, the majority lying at less than 13", but with extremes ranging from just below the surface of the ground, where they are sometimes exposed to freezing temperatures, to a possible extreme depth of 30", where the temperatures are relatively equable"; (p. 140) "at 6" deep . . . 4°C. or in exceptional years even lower . . . probable range of temperature during hibernation between 0° and 20°"; (p. 137) "It is probable that individuals and species which select shallow hibernating places frequently undergo far greater ranges of temperature than those indicated here . . . In the course of an ordinary winter night, temperatures frequently fall below 0°C., while in exceptional seasons the temperatures may fall as low as −10·5°C."

Cowles and Bogert (1944, p. 294) noted that reptiles living in a Californian environment with great extremes of temperature were not voluntarily active below 16°C., and (1944, p. 279) that the lizard *Dipsosaurus dorsalis dorsalis* exposed to a temperature slightly below 8°C. was torpid and remained helpless up to 14°C., not walking with well-co-ordinated movements until the temperature was raised to 24°C.

These observations, although made under widely different conditions, indicate that reptiles seek a considerable cover to avoid freezing temperatures at the surface. Dulhunty's experiment (1947), made at an elevation of 6,200 feet, which must be regarded as typical of the high plateau covered by snow for eight or nine months of the year, shows that the minimum winter temperature a foot below the surface is slightly more than 2° F. above freezing-point, so that hibernating reptiles at this

depth have at no time to undergo the risk of formation of ice crystals in the body, and almost certain death. This freezing would not occur even at 32°F. because of the essential presence in the body fluids of substances which lower the freezing-point. Mount Kosciusko reptiles almost certainly hibernate between depths of nine inches and three feet, where, as shown by Dulhunty, they would have a margin of from 2°F. to 4·5°F. above freezing-point. Although the minimum temperatures of 34°F. and 36·5°F. recorded at these two depths must occur for only part of the winter, it seems certain that they are approached over most of the season, the temperature of 32°F. being rapidly established at the ground surface. A margin above freezing-point is therefore essential because, while reptiles can successfully endure temperatures below this point for some time, exposure for months to freezing conditions could only be expected to cause death from chilling with formation of ice crystals in the body, increased viscosity of body fluids, checked metabolism, and other disadvantageous physical and chemical changes. Dulhunty gives the average depth of soil on the slopes and hillsides as six to eighteen inches, but undoubtedly deeper soil would be available in patches if sought by reptiles for hibernation purposes. The snow cover serves an essential purpose in preventing much water from circulating through the dark humus-laden or peat-like soil and thus increasing conductivity.

It may be of interest to note here that amphibians may show great tolerance to cold. McClure (1943, pp. 265–6) gives a remarkable account of great numbers of the salamander *Ambystoma tigrinum* migrating over snow to White Water Lake, Nebraska, at temperatures just below or just above freezing-point.

IV. BIBLIOGRAPHY.

COPLAND, STEPHEN J., 1946.—Geographic Variation in the Lizard *Hemiergis* (Fitzinger). PROC. LINN. SOC. N.S.W., 70 (3-4) : 62-92.

COWLES, RAYMOND B., 1941.—Winter Activities of Desert Reptiles. *Ecology*, 22 (2) : 125-140.

————, and BOGERT, CHARLES MITCHILL, 1944.—A Preliminary Study of the Thermal Requirements of Desert Reptiles. *Amer. Mus. Nat. Hist.*, 83 (5) : 267-296.

DULHUNTY, J. A., 1947.—Sub-surface Peat Temperatures at Mt. Kosciusko, N.S.W. PROC. LINN. SOC. N.S.W., 71 (5-6) : 292-295.

KINGHORN, J. R., 1932.—Herpetological Notes, No. 4. *Rec. Aust. Mus.*, 18 (7) : 355-363.

LOVERIDGE, ARTHUR, 1934.—Australian Reptiles in the Museum of Comparative Zoölogy, Cambridge, Massachusetts. *Bull. Mus. comp. Zool.*, 77 (6) : 243-383.

McCLURE, H. ELLIOTT, 1943.—Salamanders and Snow. *Ecology*, 24 (2) : 265-266.

SMITH, MALCOLM A., 1937.—A Review of the Genus *Lygosoma* (Scincidae : Reptilia) and its Allies. *Rec. Ind. Mus.*, 39 (3) : 213-234.

STEBBINS, ROBERT C., 1944.—Field Notes on a Lizard, the Mountain Swift, with Special Reference to Territorial Behavior. Ibid., 25 (2) : 233-245.

THE INFLUENCE OF MOLYBDENUM AND VANADIUM ON NITROGEN FIXATION BY *CLOSTRIDIUM BUTYRICUM* AND RELATED ORGANISMS.

By H. L. JENSEN, Macleay Bacteriologist to the Society, and DONALD SPENCER, B.Sc.

(*From the Department of Bacteriology, University of Sydney.*)

(Plate vii.)

[Read 26th March, 1947.]

INTRODUCTION.

The fixation of elementary nitrogen by *Azotobacter* is strongly accelerated by small quantities of molybdenum, as shown by Bortels (1930, 1936), Birch-Hirschfeld (1932), Kluyver and van Reenen (1933), Burk and Horner (1935), and Horner *et al.* (1942). By means of a manometric technique, Burk and Horner (1935) were able to detect a stimulating effect of molybdenum in a concentration as minute as 10^{-11} molar, or about 0·001 microgram per litre of medium. Molybdenum acts as a specific catalyst and can be replaced only by vanadium which at optimal concentration shows an effect of about one-half to two-thirds of that of molybdenum (Bortels, 1933, 1936; Burk and Horner, 1935; Horner *et al.*, 1942). Burk and Horner (1935) tested 22 other elements, mostly heavy metals, with negative results, and Bortels (1936) more than 40 (not specified). A stimulating effect of tungsten has sometimes been reported, but this was shown by Horner *et al.* (1942) to be spurious and due to the difficulty of separating tungsten and molybdenum completely. Earlier findings of stimulation of *Azotobacter* by other elements, such as manganese, titanium, thorium, uranium, etc., may probably be reduced to a similar cause.

The evidence is somewhat less clear-cut as regards the assimilation of combined nitrogen by *Azotobacter*. Birch-Hirschfeld (1932) found no influence of molybdenum on growth with nitrate. Burk and Horner (1935) made the same statement, but found a small acceleration of growth with ammonia, and a still smaller one with urea. Bortels (1936), on the other hand, found that molybdenum promoted the uptake of nitrate and permitted the fixation of nitrogen in the presence of nitrate, ammonia and asparagin. Horner and Allison (1944) confirmed this for nitrate and asparagin. Results found by Wilson *et al.* (1943) suggest that this discrepancy may be explained through previous adaptation of *Azotobacter* to nitrate.

There seems to be only one positive observation on record regarding the influence of molybdenum on the anaerobic nitrogen-fixing bacteria: *Clostridium butyricum* and related species. Bortels (1936) found in a single experiment with a pure culture of these organisms that the gains of nitrogen were increased some 2 to 2½ times by small doses of molybdenum and vanadium. Much earlier, Krzemieniewski (1908) had stated that humic acid stimulates nitrogen fixation by butyric acid bacilli as well as *Azotobacter*, in which the effect of humic acid has later been found to be chiefly due to molybdenum. Since there is some evidence that the clostridia may, by virtue of their wider distribution and usually greater abundance in natural habitats, equal or exceed the more efficient but less numerous *Azotobacter* as agents of biological nitrogen fixation, we have subjected this problem to a more detailed investigation.

The nutrition and especially the nitrogen fixation process of *Cl. butyricum* present several obscure aspects. Unlike *Azotobacter*, which can synthesize all its organic growth-factors, the clostridia demand certain preformed growth-compounds. No systematic study of the requirements of *Cl. butyricum* appears to have been undertaken.

For the closely related *Cl. acetobutylicum*, of which some strains are also able to fix nitrogen (McCoy *et al.*, 1928), the essential accessory factors for growth in a synthetic medium with ammonia- or amino-nitrogen have been shown by Oxford *et al.* (1940), Rubbo *et al.* (1941) and Lampen and Peterson (1943) to be biotin and *p*-aminobenzoic acid. Lampen and Peterson found a strain of *Cl. butyricum* that grew well with biotin as the only growth-compound. Woolley *et al.* (1939) studied an unidentified growth-factor, probably a mixture of biotin and *p*-aminobenzoic acid, which supported growth of *Cl. acetobutylicum* and two strains of *Cl. butyricum*, but not of a third strain of the *pasteurianum*-type, probably identical with the one received by us (cf., below).

The need of nitrogen-fixing clostridia for organic growth-compounds thus appears clearly established, but the medium for nitrogen fixation experiments has nearly always been some modification of the synthetic and, if pure, growth-compound-free glucose solution used by Winogradsky (1895). Growth in such a medium may occur only if a sufficient amount of growth-compounds is carried over with the inoculum, and the size of this is rarely stated. Bredemann (1909b), for instance, used 10 ml. of culture fluid per litre of medium, and McCoy *et al.* (1928) state that as inocula they used "measured amounts of 24 hour corn mash cultures"; the amounts were not specified, and the authors make the significant remark that inocula from previous cultures in Winogradsky's or other synthetic media were weak and uncertain. An inoculum large enough to contain sufficient growth-compounds for the subculture would be quite likely also to provide an adequate supply of molybdenum. This was apparently not the case in the experiment of Bortels (1936), who states that the mother-culture was grown in molybdenum-free medium, but it may explain the negative result of an earlier tentative experiment by one of us (Jensen, 1941), in which it was found necessary to use an inoculum of several drops of glucose broth culture per 50 ml. solution in order to start growth.

The quantity of nitrogen fixed by *Cl. butyricum*, especially the *pasteurianum*-type, has usually been found to vary between 1 and 3 mgm. per gm. fermented sugar (Winogradsky, 1895; Pringsheim, 1908; Bredemann, 1909b; Lantsch, 1921; McCoy *et al.*, 1928; Willis, 1934; Sjolander and McCoy, 1937). Higher yields have rarely been observed. Bredemann (1909b) found occasional gains up to 6 mgm.; McCoy *et al.* (1928) showed that the slowly-fermenting strains of the *saccharobutyricum*-type could fix from 4·3 to 7 mgm. nitrogen per gm. sugar, and Kostytchev (1924) mentions a yield of 12·5 mgm. In associated cultures of clostridia and cellulose-decomposing bacteria the yield of fixed nitrogen has repeatedly been found to reach 7 to 10 mgm. per gm. cellulose lost (Pringsheim, 1910; Jensen, 1941).

It is probable that the strongest nitrogen fixation may occur if the medium contains adequate supplies of organic growth-compounds and of molybdenum but a minimum of available nitrogen which tends to inhibit fixation, as shown by Winogradsky (1895) and Omeliansky (1916). Therefore, we have endeavoured to develop a medium deficient in molybdenum and nitrogen while providing the organic growth-factors needed by *Cl. butyricum*.

<p style="text-align:center">EXPERIMENTAL.</p>

Methods and Organisms.—Eight freshly isolated strains of *Cl. butyricum* were tested; four of these (Nos. 1, 3, 6a and 6b) were isolated from soil, three (Nos. 7a, 7b and 8) from garden compost, and one (No. 5) from flax straw. Enrichment cultures were made by inoculation of Winogradsky's solution with soil or compost suspension or liquid from retting flax, and incubation at 30°C. after pasteurization for 5 to 10 minutes at 80°C. When gas evolution appeared and typical clostridia were seen by microscopic examination (sometimes after two or three transfers in the same medium), subcultures were made in potato-medium (test-tubes with 12–15 ml. tap water, a two-inch deep layer of small pieces of peeled potatoes, and some calcium carbonate). These cultures always showed vigorous fermentation, smelt of butyric acid, and showed an abundance of clostridia staining blue with iodine after 24 hours at 30° or 37°C. Pasteurization was then repeated, and plate cultures were made on glucose agar with

lucerne-root-extract and incubated in hydrogen atmosphere in an anaerobic jar at 30°C. Isolated colonies of microscopically pure appearance were transferred to tubes of potato medium which supported good growth of the pure cultures in atmospheric air if the medium was boiled and cooled immediately before inoculation. The same medium, sometimes with addition of a small quantity of soil, was used for maintenance of the cultures. The purity of these was tested by cultivation aerobically in nutrient broth, in glucose-peptone solution, and on plates of nutrient agar; slopes of fresh glucose agar often showed growth of the clostridia in the condensation-water, as also observed by Bredemann (1909b).

Besides these fresh isolates we have tested a strain of the *pasteurianum*-type (originally isolated by Winogradsky) from the Department of Agricultural Bacteriology, University of Madison, U.S.A., and a strain of *Cl. acetobutylicum* from the Department of Bacteriology, University of Melbourne. These two strains are in the following tables called "W" and "B", respectively.

Morphologically, all strains showed the typical appearance: big rods with rounded ends, mostly single or in pairs, rarely in chains of 3 or 4 cells, actively motile, Gram-positive when young but rapidly becoming Gram-negative, and developing into typical spindle-shaped clostridia that stain blue with iodine and contain oval, subterminal endospores. The vegetative cells measured $0.5-1.2 \times 2-8\mu$, sometimes up to 10μ long and 2.5μ thick in the clostridium-stage, and the endospores $1.0-1.2 \times 1.5-1.8\mu$. In some strains, for instance, Nos. 1 and 3, the cells were predominantly long and slender, in No. 5 short and thick, almost lemon-shaped in the clostridium-stage.

The fermentation reactions of the strains were tested towards some of the compounds most likely to distinguish between the different types of butyric acid bacilli according to McCoy *et al.* (1930). The medium was Winogradsky's solution (see below) with 0.2% ammonium lactate, 0.2% potato-extract-concentrate, and 1.0% carbon compound, but no calcium carbonate. Test-tube cultures incubated four days at 35°C. in hydrogen atmosphere showed the following reactions:

Carbon Compound.	Fermentation (Acid and Gas) by Strain No.									
	1	3	5	6a	6b	7a	7b	8	W	B
Mannite	+	-	?	+	+	+	+	+	+	+
Lactose	+	+	+	+	+	-	-	+	-	+
Starch	+	-	+	+	+	...	-	+	-	+

Strains 1, 5, 6a, 6b and 8 appear to represent the starch-fermenting *saccharobutyricum*-type and strains 7a and 7b the *pasteurianum*-type, of which strain W is the prototype, while strain 3 seems to represent an atypical form (McCoy *et al.* (1930) found only one strain among 35 unable to ferment mannite. In another series of investigations, Sjolander and McCoy (1937) found 5 out of 20 strains unable to ferment mannite, but these all fermented starch.) It also differs from the others in causing a vigorous reduction of nitrate (0.2% NaNO₃ in Winogradsky's solution, incubated in hydrogen atmosphere) to ammonia with formation of small amounts of nitrite, probably as an intermediate product.

The basal medium for the nitrogen-fixation experiments was a modification of Winogradsky's solution: glucose 20.0 gm., K₂HPO₄ 0.5 gm., KH₂PO₄ (sometimes omitted) 0.5 gm., MgSO₄ 0.1 gm., NaCl 0.1 gm., FeSO₄ 0.01 gm., MnSO₄ 0.01 gm. (this was found unnecessary and was often omitted), CaCO₃ 4.0 or 5.0 gm., distilled water 1,000 ml. The amount of calcium carbonate was reduced from 30 gm., as used by Winogradsky and most others, in order to minimize the amounts of molybdenum and other trace element impurities that might be introduced with it. The chemicals were of ordinary analytical purity.

Some difficulty was at first experienced in obtaining growth with small inocula. Even in solution with combined nitrogen, biotin and *p*-aminobenzoic acid (the medium

of Lampen and Peterson, 1943), growth from an inoculum of 0·01 ml. potato-medium culture per 10 ml. solution took place only irregularly and after a long lag period. In this connection it is noteworthy that Rubbo *et al.* (1941) and Lampen and Peterson (1943) used inocula of about 0·1 ml. per 5 or 10 ml. of medium, and that Oxford *et al.* (1940) found the growth of *Cl. acetobutylicum* in synthetic solution with biotin and an unknown growth-factor (probably *p*-aminobenzoic acid) accelerated by small additional amounts of cystein, valin and methionin. On the other hand, prompt and vigorous growth within 24 hours at 37°C. was obtained when potato extract was added to the medium, and the same effect was shown by a potato-extract-concentrate from which most of the nitrogenous and mineral constituents had been removed, and which was prepared as follows:

Five hundred gm. of peeled and finely-chopped potatoes were heated for 3 to 4 hours in the steamer with one litre of tap water; the liquid was strained off, and the residue was washed with hot water to make one litre of extract, which was filtered on the Buchner funnel to remove the suspended solid matter. The clear extract was concentrated to about 50 ml. by evaporation on the water-bath, 600 ml. ethyl alcohol were added, the mixture was allowed to stand for at least 24 hours, and the voluminous precipitate was removed by filtration. The alcohol was now distilled off and the extract was finally brought to a volume of 50 ml., sterilized by autoclaving, and stored at refrigerator temperature. Two batches of extract were used in the course of the work, in the following called G.F.1 and G.F.2; the second had a somewhat higher nitrogen and growth-factor content than the first.

For the nitrogen-fixation experiments, 0·2 to 0·5% G.F.-solution was added to the glucose solution, together with one γ of pure biotin (from Lilley & Co.) per litre, and a similar quantity of *p*-aminobenzoic acid. This basal medium was highly deficient in available molybdenum and vanadium, as shown by several tests with a vigorously nitrogen-fixing strain of *Azotobacter chroococcum*. Table 1 gives the results; especially G.F.2 appears almost devoid of molybdenum and vanadium, which seem to be carried down almost quantitatively in the alcohol-precipitate.

TABLE 1.

Response of Azotobacter chroococcum *to Molybdenum and Vanadium added to Winogradsky's Solution.*

Exp. No.	Medium and Incubation.	Mgm. N per Culture. a. b.	Gain of N, mgm. a. b.
I	40 ml. solution, 0·2% G.F.1. Initial N-content, 0·48 mgm. Inc. 7 d. 30° C.		
	Cultures in : Basal medium (control)	1·59– 1·63	1·11– 1·15
	Do. +10 p.p.m. Na₂MoO₄	11·57–11·95	11·09–11·47
	Do. +10 ,, NH₄VO₃	8·38– 8·46	7·90– 7·98
II	25 ml. solution, 0·5% G.F.1. Initial N-content, 0·32 mgm. Inc. 8 d. 30° C.		
	Cultures in : Basal medium (control)	1·11– 1·53	0·79– 1·21
	Do. + 1·4 p.p.m. VOSO₄	3·91– 4·10	3·59– 3·78
III	25 ml. solution, 0·4% G.F.2. Initial N-content, 0·70 mgm. Inc. 7 d. 30° C.		
	Cultures in : Basal medium (control)	0·84– 0·85	0·14–0·15
	Do. +10 p.p.m. VOSO₄	4·30	3·60
IV	20 ml. solution with and without 0·2% G.F.2. Inc. 10d. 22–25° C. Initial N-content, –G.F., 0·15 mgm., +G.F., 0·44 mgm.		
	Cultures in : Basal medium –G.F.	0·26– 0·29	0·11– 0·14
	Do. +4·6 p.p.m. Mo	2·73	2·58
	Basal medium +G.F.	0·52– 0·56	0·08– 0·12
	Do. +0·002 p.p.m. Mo	1·67	1·23
	Do. +4·6 ,, Mo	2·87	2·43

The medium was used in portions of 50 ml. in 100-c.c. round flasks or Erlenmeyer flasks of Pyrex glass, which before use were cleaned with a hot solution of potassium bichromate and sulphuric acid, thoroughly washed, and boiled in distilled water; inconsistent results with the molybdenum-free basal medium were sometimes found if this cleansing was omitted. Molybdenum was added as sodium molybdate, vanadium as ammonium vanadate (NH_4VO_3) or vanadyl sulphate ($VOSO_4$). The inoculum consisted of one or two drops of a vigorously fermenting 24-hours culture in potato-medium. Growth usually appeared within two days, whereas smaller inocula either showed a long lag period or failed to grow altogether. Very little available molybdenum and vanadium was carried over with the inoculum, as shown by an assay with *Azotobacter*:

Duplicate 25-ml. portions of Winogradsky's solution, without potato-extract, and with sucrose instead of glucose, were given additions of 2, 5 and 10 drops of potato-culture of strain W, sterilized, inoculated with *Az. chroococcum*, and incubated 10 days at 30–32°C. Nitrogen determinations showed the following results:

Addition to Medium.	Nitrogen Fixed. Mgm.	
	a	b
Nil (control)	0·28	0·34
2 drops of *Clostridium*-culture	0·28	0·43
5 ,, ,, ,, ,, ...	0·30	0·34
10 ,, ,, ,, ...	0·36	0·37
10 p.p.m. Na_2MoO_4 (0·12 mgm. Mo per culture)	4·20	4·80

The cultures of clostridia were incubated in big vacuum desiccators or anaerobic jars with an atmosphere of nitrogen gas that had first been passed through alkaline pyrogallol. The temperature of incubation was normally 30°C.; in a few instances, fluctuations in the temperature of the incubation-room caused rises to 32–35°C., which did not appear to make any difference to the results. Duplicate flasks analysed immediately after inoculation served as controls showing the initial nitrogen-content. Uninoculated flasks sometimes showed a small but definite loss of nitrogen during incubation (cf., Löhnis, 1930), and also occasional cultures that failed to grow (Table 5, II–III); therefore the initial nitrogen-content was subtracted from that of the incubated cultures to give the net gain of nitrogen. This was determined by the Kjeldahl method, with selenium as a catalyst; N/28 sulphuric acid and sodium hydroxide, with methyl red and methylen blue as indicator, were used for the titration. In some cases an aliquot of the culture was taken for determination of residual glucose by the method of Lane and Eynon, adapted for small quantities by Cole. All subsequent data, unless otherwise stated, refer to 50 ml. of medium (1 gm. of glucose).

The Effect of Molybdenum and Vanadium on Nitrogen Fixation by Various Strains.— The data collected in Table 2 show that all the strains are able to fix small quantities of nitrogen in the basal medium, but the gains are strongly increased, mostly three- to sixfold, by the addition of 5 or 10 parts per million of sodium molybdate. The upper and lower limits of fixation by the nine strains of *Cl. butyricum* are:

	−Mo	+Mo
Lowest gain, mgm. N	0·08	1·53
Highest ,, ,, ,, ...	0·96	3·95
Mean ,, ,, ,, ...	0·48	2·70

Cl. acteobutylicum fixes rather less nitrogen, as also found by McCoy *et al.* (1928), but the stimulating effect of molybdenum is very marked.

Vanadium, either as sulphate or as vanadate, has no influence on strains 1, 3, 5, 8 (probably), and *Cl. acetobutylicum*, but gives considerable stimulation of the others. In strains 6a and 6b it even appears equal to molybdenum, while in 7a, 7b and W its effect is about one-half to two-thirds of that of molybdenum, as in *Azotobacter*. The beneficial effect of the two elements became apparent at an early stage of growth, by increased gas formation and turbidity. Plate vii shows the appearance of some typical cultures. The results thus confirm the finding of Bortels (1936), except that not all strains respond to vanadium.

TABLE 2.

Nitrogen Fixation by Various Strains of Cl. butyricum *and* Cl. acetobutylicum.

Exp. No.	Medium and Incubation.	Mgm. N per Culture. a. b.	Gain of N, mgm. a. b.
I	*Strain* 1.—0·5% G.F.1. Inc. 14 d. 30° C. Initial N-content, 0·80 mgm.		
	Cultures in : Basal medium (control)	0·88–0·92	0·08–0·12
	Do. +10 p.p.m. Na₂MoO₄	3·31–3·99	2·51–3·19
II	*Strain* 3.—As (1).		
	Cultures in : Basal medium (control)	0·88–0·89	0·08–0·09
	Do. +10 p.p.m. Na₂MoO₄	3·70–3·88	2·90–3·08
III	*Strain* 3.—0·2% G.F.2. Inc. 11 d. 30° C. Initial N-content, 0·96 mgm.		
	Cultures in : Basal medium (control)	1·13–1·23	0·17–0·27
	Do. +5 p.p.m. Na₂MoO₄	3·02–3·04	2·06–2·08
	Do. +5 ,, VOSO₄	1·15–1·23	0·19–0·27
IV	*Strain* 1.—0·4% G.F.1. Inc. 14 d. 30° C. Initial N-content, 0·64 mgm.		
	Cultures in : Basal medium (control)	0·97–1·08	0·33–0·39
	Do. +10 p.p.m. Na₂MoO₄	3·84	3·20
	Do. +1·5 ,, VOSO₄	1·12	0·48
	Do. +10 ,, Na₂WO₄*	2·98–3·56	2·34–2·92
V	*Strain* 1.—0·4% G.F.2. Inc. 14 d. 30° C. Initial N-content, 1·72 mgm.		
	Cultures in : Basal medium (control)	1·95–1·95	0·23–0·23
	Do. +10 p.p.m. Na₂MoO₄	3·36–3·40	1·64–1·68
	Do. +4 ,, NH₄VO₃	2·04–2·05	0·32–0·33
VI	*Strain* 5.—0·2% G.F.1. Inc. 14 d. 37° C. Initial N-content, 0·54 mgm.		
	Cultures in : Basal medium (control)	1·33–1·50	0·79–0·96
	Do. +10 p.p.m. Na₂MoO₄	3·53–4·49	2·99–3·95
	Do. +10 ,, VOSO₄	1·23–1·28	0·69–0·74
VII	*Strain* 5.—0·4% G.F.2. Inc. 14 d. 30° C. Initial N-content, 1·72 mgm.		
	Cultures in : Basal medium (control)	1·95–2·04	0·23–0·32
	Do. +10 p.p.m. Na₂MoO₄	3·25–3·63	1·53–1·91
	Do. + 4 ,, NH₄VO₃	1·94–2·48	0·22–0·76
VIII	*Strain* 6a.—0·4% G.F.1. Inc. 14 d. 30° C. Initial N-content, 0·75 mgm.		
	Cultures in : Basal medium (control)	1·17–1·38	0·42–0·63
	Do. +10 p.p.m. Na₂MoO₄	2·55–2·73	1·80–1·98
	Do. +10 ,, VOSO₄	2·50–3·16	1·75–2·41
IX	*Strain* 6b.—As VIII.		
	Cultures in : Basal medium (control)	1·27–1·30	0·52–0·55
	Do. +10 p.p.m. Na₂MoO₄	2·52–3·25	1·77–2·50
	Do. +10 ,, VOSO₄	2·61–2·74	1·86–1·99
X	*Strain* 7a.—0·2% G.F.2. Inc. 12 d. 30° C. Initial N-content, 0·96 mgm.		
	Cultures in : Basal medium (control)	1·32–1·44	0·36–0·48
	Do. + 5 p.p.m. Na₂MoO₄	4·02–4·46	3·06–3·50
	Do. + 5 ,, VOSO₄	3·09–3·17	2·13–2·21
XI	*Strain* 7b.—As X.		
	Cultures in : Basal medium (control)	1·50–1·58	0·54–0·62
	Do. + 5 p.p.m. Na₂MoO₄	3·84–4·49	2·98–3·53
	Do. + 5 ,, VOSO₄	2·60–2·90	1·64–1·94

* *Cf.* Table 5.

TABLE 2.—*Continued.*

Nitrogen Fixation by Various Strains of Cl. butyricum *and* Cl. acetobutylicum.

Exp. No.	Medium and Incubation.	Mgm. N per Culture. a. b.	Gain of N, mgm. a. b.
XII	*Strain 8.*—As X and XI.		
	Cultures in Basal medium (control)	1·50—(lost)	0·54
	Do. + 5 p.p.m. Na₂MoO₄	3·61-3·63	2·65-2·67
	Do. + 5 ,, VOSO₄	1·51-2·13	0·55-1·17
XIII	*Strain W.*—0·4% G.F.1. Inc. 14 d. 30° C. Initial N-content, 0·64 mgm.		
	Cultures in: Basal medium (control)	1·19-1·39	0·55-0·75
	Do. +10 p.p.m. Na₂MoO₄	4·31-4·44	3·67-3·80
	Do. + 4 ,, NH₄VO₃	2·89-3·19	2·25-2·55
XIV	*Strain W.*—0·4% G.F.2. Inc. 12 d. 30° C. Initial N-content, 1·72 mgm.		
	Cultures in: Basal medium (control)	2·47-2·57	0·75-0·85
	Do. +10 p.p.m. Na₂MoO₄	5·30-(>4·30)*	3·58-(>2·58)
	Do. + 5 ,, VOSO	3·32-3·42	1·60-1·70
XV	*Cl. acetobutylicum* (B). 0·2% G.F.2. Inc. 12 d. 32-35° C. Initial N-content, 1·05 mgm.		
	Cultures in: Basal medium (control)	1·25-1·30	0·20-0·25
	Do. +10 p.p.m. Na₂MoO₄	2·53-2·64	1·48-1·59
	Do. +10 ,, VOSO₄	1·26-1·28	0·21-0·23

* Some of the ammonia was lost during the distillation.

A few additional tests were made with a strain of *Aerobacillus polymyxa*, usually regarded as identical with *Bac. asterosporus*, which Bredemann (1909a) found able to fix nitrogen. No fixation could be detected in our cultures, either aerobically or in nitrogen-atmosphere, although some growth took place. It is possible that nitrogen-fixing power might be restored by soil passage as found by Bredemann.

Residual glucose was determined in some of the cultures and the gains of nitrogen calculated per gm. of sugar that had disappeared. These results are shown in Table 3, and agree with the current statement that the clostridia mostly fix from one to three mgm. nitrogen per gm. consumed sugar; indeed the higher of these values is only reached or exceeded where molybdenum is added. The same is the case in several other experiments (Table 2, VI, X, XI, XIII, XIV; Table 4, III), where the fixation ranges between 3 and 4 mgm. per 50 ml. with 1 gm. glucose.

It is possible, however, that the yields of nitrogen are really higher than they appear, particularly in the molybdenum-deficient media, since some of the consumed sugar is probably not used for nitrogen fixation but for growth with the combined nitrogen that the potato-extract contains. It was shown that this nitrogen is available for growth and fermentation, by cultivating two strains for 12 days at 30°C. in a hydrogen atmosphere and in a solution containing 1·0% glucose, 0·2% G.F.2, and 10 p.p.m. sodium molybdate. The result was as follows:

	Strain 1.		Strain 3.	
	—Mo	+Mo	—Mo	+Mo
Mgm. glucose consumed per 50 ml. medium—				
a	..144	158	158	290
b	..146	164	171	300

It is noteworthy that the sugar consumption by one of the strains is nearly doubled by the addition of molybdenum, although, of course, no nitrogen was fixed (initial nitrogen-content 1·00 mgm., after incubation 0·96-1·10 mgm.). A correction for this effect of the combined nitrogen would obviously make the economy of nitrogen fixation appear higher, especially in the absence of molybdenum, but it is uncertain whether

TABLE 3.

Consumption of Glucose and Fixation of Nitrogen per Gram of Glucose consumed. (Cf., Table 2.)

Strain and Exp. No.	Control.		+Mo.		+V.	
	Glucose Consumed, mgm.	N Fixed, mgm.	Glucose Consumed, mgm.	N Fixed, mgm.	Glucose Consumed, mgm.	N Fixed, mgm.
Strain 1, Exp. I—						
a.	170	0·5	649	3·9	—	—
b.	146	0·8	627	5·1	—	—
Strain 3, Exp. II—						
a.	170	0·5	676	4·3	—	—
b.	140	0·6	710	4·3	—	—
Strain 3, Exp. III—						
a.	148	1·1	742	2·8	176	1·1
b.	170	1·6	718	2·9	198	1·4
Strain 7a, Exp. X—						
a.	323	1·1	997	3·1	997	2·2
b.	509	0·9	997	3·5	997	2·2
Strain 7b, Exp. XI—						
a.	281	1·9	997	3·0	997	1·6
b.	313	2·0	997	3·5	997	1·9
Strain 8, Exp. XII—						
a.	227	2·4	997	2·7	315	1·7
b.	—	—	997	2·7	494	2·4
Cl. acetobutylicum, Exp. XV—						
a.	334	0·6	815	2·0	378	0·6
b.	365	0·6	840	1·8	362	0·6

the amount of sugar used up in this way is the same in a hydrogen atmosphere and where nitrogen gas is available for fixation.

Winogradsky (1895), Pringsheim (1908) and Omeliansky (1916) observed that the yield of nitrogen fixed per gm. fermented sugar increased with decreasing glucose concentration of the medium. A test was performed with strain W in order to ascertain if this also applies when an adequate supply of molybdenum is given. The medium contained 0·4% G.F.2, 10 p.p.m. sodium molybdate, and four concentrations of glucose, and had an initial nitrogen content of 1·40 mgm. The following results were found after incubation for 14 days at 32–35°C.:

Per cent. glucose in medium	0·5	1·0	2·0	3·0
Gain of nitrogen, mgm.—				
a	1·52	2·87	3·53	3·93
b	1·48	2·22	3·43	3·99
Consumption of glucose, mgm.—				
a	278	480	926	1,069
b	278	480	926	1,052
Mgm. nitrogen fixed per gm. glucose consumed—				
a	5·5	4·9	3·8	3·7
b	5·3	4·6	3·7	3·8

There is a clear indication that the lower concentrations of sugar are used more economically. The apparent difference is not very great, but here again some glucose has doubtless been used at the expense of the combined nitrogen, and since the amount of this was constant, a correction would particularly increase the yields of nitrogen with the lower sugar concentrations. Phenomena of this kind might explain the high

economy of nitrogen fixation in associated cultures of clostridia and cellulose-decomposing bacteria, where the concentration of sugar produced from the cellulose is kept at a low level by the clostridia and the available nitrogen-compounds removed by the cellulose-decomposers.

The Effective Range of Concentration of Molybdenum and Vanadium.—In the previous experiments the concentrations of molybdenum corresponded to 2·33–4·66 p.p.m., and those of vanadium to 0·47–3·18 p.p.m. These amounts are very large in comparison with those sufficient for *Azotobacter*, and the effect of varying concentrations was tested next. A preliminary experiment with strain 3 showed practically the same gains of nitrogen at concentrations of molybdenum ranging from 0·01 to 5·0 p.p.m., but this experiment was vitiated by an abnormally strong fixation in one of the control cultures. The results of the main experiments are seen in Table 4.

TABLE 4.
Effective Range of Concentration of Molybdenum and Vanadium.

Exp. No.	Strain, Medium and Incubation.	Mgm. N per Culture. a. b.	Gain of N, mgm. a. b.
I	*Strain 3.*—0·4% G.F.1. Initial N-content, 0·84 mgm. Inc. 14 d. 30–32° C.		
	Cultures in : Basal medium (control)	1·31–1·34	0·47–0·50
	Do. +0·00002 p.p.m. Mo	0·97–1·15	0·13–0·31
	Do. +0·0001 ,, Mo	1·20–1·23	0·36–0·39
	Do. +0·0005 ,, Mo	1·49–1·75	0·65–0·91
	Do. +0·002 ,, Mo	1·75–2·05	0·91–1·21
	Do. +0·01 ,, Mo	3·18–3·20	2·34–2·36
II	*Strain W.*—0·25% G.F.2. Initial N-content, 1·47 mgm. Inc. 14 d. 30–35° C.		
	Cultures in : Basal medium (control)	2·00–2·03	0·56–0·67
	Do. +0·0001 p.p.m. Mo	1·75–2·48	0·28–1·01
	Do. +0·0005 ,, Mo	2·05–2·25	0·58–0·78
	Do. +0·002 ,, Mo	2·61–2·66	1·14–1·19
	Do. +0·01 ,, Mo	3·65–4·15	2·18–2·68
	Do. +0·1 ,, Mo	4·23–4·43	2·76–2·96
	Do. +1·0 ,, Mo	4·32–4·40	2·85–2·93
III	*Strain W.*—0·2% G.F.2. Initial N-content, 1·00 mgm. Inc. 14 d. 30–35° C.		
	Cultures in : Basal medium (control)	1·80–1·86	0·80–0·86
	Do. +0·002 p.p.m. V	2·75–3·01	1·75–2·01
	Do. +0·005 ,, V	3·01–3·11	2·01–2·11
	Do. +0·01 ,, V	3·24–(lost)	2·24
	Do. +0·1 ,, V	3·29–3·51	2·29–2·51
	Do. +1·0 ,, V	3·30–3·56	2·30–2·56
	Do. +4·6 ,, Mo	4·46–4·95	3·46–3·95
IV	*Strain W.*—0·2% G.F.2. Initial N-content, 0·89 mgm. Inc. 12 d. 35° C.		
	Cultures in : Basal medium (control)	1·42–1·43	0·53–0·54
	Do. +0·0002 p.p.m. V	1·71–1·92	0·82–1·03
	Do. +0·001 ,, V	2·37–2·61	1·48–1·72
	Do. +4·6 ,, Mo	3·00–3·16	2·11–2·16
V	*Strain W.*—0·2% G.F.2. Initial N-content, 0·78 mgm. Inc. 12 d. 30° C.		
	Cultures in : Basal medium (control)	1·57–1·64	0·79–0·86
	Do. +0·0001 p.p.m. V	1·63–1·74	0·85–0·96
	Do. +0·0002 ,, V	1·86–1·87	1·08–1·09
	Do. +0·002 ,, Mo	2·39–(lost)	1·61
	Do. +do. +0·0001 p.p.m. V	2·30–2·66	1·52–1·88
	Do. +0·004 p.p.m. Mo	2·75–2·82	1·97–2·04
	Do. +do. +0·0002 p.p.m. V	2·94–2·96	2·16–2·18
	Do. +0·100 p.p.m. Mo	3·72–3·75	2·94–2·97

With both strains a molybdenum concentration of 0·01 p.p.m., or roughly 10^{-7} molar, has an almost optimal effect, while 0·002 p.p.m. approximately doubles the fixation in the control medium, and the effect of 0·0005 p.p.m. seems detectable in strain 3. The figures are comparable to those found by Horner et al. (1942) for *Azotobacter*, although this seems to have a somewhat wider range of effective concentration (1 p.p.m. had optimal effect, and 0·00001–0·0001 p.p.m. had still a detectable effect in cultures 6 days old). The very small amounts of molybdenum, 0·00002–0·0001 p.p.m., show no effect at all. This suggests that the clostridia are capable of some slight nitrogen fixation in a medium devoid of available molybdenum, and that the molybdenum begins to catalyze the process when it is present in a concentration near or slightly above 0·5γ per litre of medium, or 0·5 × 10^{-8} molar. As to vanadium, the effect of 0·002 p.p.m. is still some 75% of the optimum, and 0·0002 p.p.m., or roughly 0·4 × 10^{-8} molar concentration, causes a detectable stimulation. Its active range thus seems to extend a little further than that of molybdenum, although it is less effective at optimum concentration. There is finally in Exp. No. IV a suggestion of an additive effect of 0·004 p.p.m. molybdenum and 0·0002 p.p.m. vanadium.

The Specificity of Molybdenum and Vanadium.—As mentioned in the introduction, no other elements have been found able to replace molybdenum and vanadium in *Azotobacter*. To see if the same is the case in the clostridia, as possible substitutes, we have tested some of the heavy metals of general physiological importance, namely, manganese, zinc, cobalt and copper, besides several elements of the same periodic groups as molybdenum and vanadium: chromium, tungsten, uranium, niobium, tantalum and bismuth. The experiments already discussed show that manganese is without effect; for instance, it was added to the basal medium in Exps. I, II, III, VI, X, XI and XII, Table 2. Also iron, which was always included, is obviously unable to replace molybdenum. The results of the tests with the other elements are seen in Table 5.

It seems quite clear that none of the elements tested can replace molybdenum and vanadium; several of them are even inhibitory, especially towards strain W. In the case of tantalum, the inhibition might indeed be due to an excess of potassium hydroxide in the stock solution of potassium tantalate; therefore, the test was repeated with a neutralized solution and a tantalum concentration of 0·5 p.p.m. This time growth took place, but the nitrogen fixation was not stimulated: gains in basal medium, 0·79–0·86 mgm., with 0·5 p.p.m. Ta, 0·81–0·82 mgm. (cf., Table 4, V).

Tungsten presents some special problems. On a previous occasion (Table 2, IV) it showed an appreciable stimulation, but this might be due to impurities of molybdenum, since the sodium tungstate also stimulated nitrogen fixation by *Azotobacter*, and this effect persisted after two recrystallizations (0·08–0·35 mgm. nitrogen was fixed per 25 ml. basal medium, 2·78–2·92 mgm. in medium with 10 p.p.m. sodium tungstate). A spectrographic examination of the twice recrystallized sodium tungstate, by Mr. A. C. Oertel, Waite Institute, Adelaide, showed the presence of molybdenum to the amount of some parts per million; if we assume 10 p.p.m., the addition of 10 mgm. of the salt per litre of medium would thus have provided 0·1γ of molybdenum, a quantity which, according to the data in Table 4, could hardly be expected to have any significant effect on the clostridia, although it might explain the stimulation of *Azotobacter*. A test was conducted with tungsten in varying concentration: 1·0, 0·1 and 0·01 p.p.m. The last quantity had no effect on *Azotobacter*, which in 20 ml. solution incubated 10 days at 22–25°C. (cf., Table 1, IV) showed the following gains of nitrogen:

Control medium   ..   ..   0·11–0·14 mgm.
Do. +0·01 p.p.m. W   ..   ..   0·12–0·15   ,,

The disappearance of the stimulating effect towards strain W with increasing dilution (Table 5, IV) suggests that the effect was really due to the small amount of molybdenum impurity, although an absolutely molybdenum-free tungsten compound would be needed to supply the final answer.

TABLE 5.

Specificity of Molybdenum and Vanadium as Catalysts of Nitrogen Fixation.

Exp. No.	Strain, Medium and Incubation.	Mgm. N per Culture a. b.	Gain of N, mgm. a. b.
I	*Strain* 1.—0·4% G.F.1. Initial N-content, 0·56 mgm. Inc. 10 d. 30° C.		
	Cultures in : Basal medium (control)	1·05–1·08	0·49–0·52
	Do. +20 p.p.m. KCr(SO₄)₂	1·00–1·07	0·44–0·51
	Do. +10 „ UO₂(NO₃)₂	1·01–1·03	0·45–0·47
	Do. +10 „ Na₂MoO₄	2·09–2·23	1·53–1·67
II	*Strain* 1.—0·25% G.F.2. Initial N-content, 1·47 mgm. Inc. 14 d. 30° C.		
	Cultures in : Basal medium (control)	1·68–1·85	0·21–0·38
	Do. +10 p.p.m. ZnSO₄	1·45–1·58	(0) –0·11
	Do. +10 „ Co(NO₃)₂	1·45–1·54	(0) –0·07
	Do. +10 „ CuSO₄	1·29–1·35	(no growth)
	Do. +10 „ Na₂MoO	2·25–2·30	0·78–0·83
III*	*Strain* W.—0·25% G.F.2. Initial N-content, 1·30 p.p.m. Inc. 13 d. 30° C.		
	Cultures in : Basal medium (control)	1·88–1·93	0·58–0·63
	Do. +1·0 p.p.m. Zn	1·78–1·90	0·48–0·60
	Do. +1·0 „ Co	1·16–1·19	(no growth)
	Do. +1·0 „ Cu	1·14–1·18	(no growth)
	Do. +1·0 „ Cr	1·83–1·92	0·53–0·62
	Do. +1·0 „ U	1·18–1·19	(no growth)
	Do. +1·0 „ Nb	1·68–1·75	0·38–0·45
	Do. +1·0 „ Ta	1·12–1·15	(no growth)
	Do. +1·0 „ Bi	1·55–1·65	0·25–0·35
	Do +1·0 „ Mo	3·45–3·53	2·15–2·23
IV	*Strain* W.—0·2% G.F.2. Initial N-content, 0·89 mgm. Inc. 12 d. 35° C.		
	Cultures in : Basal medium (control)	1·42–1·43	0·53–0·54
	Do. +1·0 p.p.m. W	2·28–2·30	1·39–1·41
	Do. +0·1 „ W	1·45–1·47	0·56–0·58
	Do. +0·01 „ W	1·36–1·37	0·47–0·48
	Do. +4·6 „ Mo	3·00–3·16	2·11–2·27

* Niobium and tantalum were added as potassium niobate and tantalate, prepared by fusing the oxides with potassium hydroxide, bismuth as nitrate, the other metals in the same form as in Exps. I-II.

Upon the whole, it thus appears that the requirement of *Cl. butyricum* for molybdenum or vanadium is as specific as that of *Azotobacter*, or rather more so, since it is not all strains of clostridia that respond to vanadium.

It might here be mentioned that the stimulating influence of materials like soil or humus preparations on nitrogen fixation by clostridia, observed by Krzemieniewsky (1908) and Willis (1934), might be partly due to molybdenum or vanadium, as suggested by Bortels (1936), and partly to organic growth compounds. When Lantsch (1921) found that humus did not increase nitrogen fixation but caused a marked reduction in the length of the lag phase in clostridia, the explanation may be that these humus preparations were deficient in molybdenum but provided organic growth factors like biotin, *p*-aminobenzoic acid, etc.

The Influence of Molybdenum and Vanadium on Growth of Cl. butyricum *with Combined Nitrogen.*—A few tests were carried out to see if molybdenum and vanadium also accelerate the growth with combined nitrogen, measured by the rate of sugar fermentation. Three strains of clostridia were grown in Lampen and Peterson's (1943) medium, with addition of 0·5% G.F.1, and some calcium carbonate to prevent inhibition of the growth by accumulation of acid. Molybdenum was added as 10 p.p.m. of sodium molybdate, and vanadium as 4 p.p.m. ammonium vanadate. Test-tubes with 10 ml.

solution were inoculated with one drop of potato-medium culture and incubated in a hydrogen atmosphere at 37°C., in one test also at 30° C., and glucose was determined in duplicate or triplicate tubes at intervals mostly of 24 hours.

TABLE 6.

Rate of Fermentation of Glucose in Solution with Combined Nitrogen.

Strain.	Medium.	Per Cent. Glucose Fermented after Days.						
		1	2	3	4	6	7	8
1	−Mo	39	72	88				
	+Mo	30	73	90				
1 (30° C.)	−Mo	7	26	37	56		89	
	+Mo	20	25	56	56		100	
3	−Mo	15	35	47	73	96		
	+Mo	28	45	78	100	100		
5	−Mo	6	38	50	50			64
	+Mo	12	40	49	53			64
W	−Mo	12	81	96				
	+Mo	6	79	96				
	+V	36	88	100				

As seen from Table 6, molybdenum has only a small and irregular influence on the rate of fermentation, and this is most noticeable in the early stages of growth, which also appeared to start earlier in the presence of molybdenum. In the case of strain W, the same shortening of the lag phase by vanadium is quite marked, but the effect already is wearing off after 48 hours. Upon the whole, the effect of molybdenum under these conditions appears quite comparable to its influence on the growth of *Azotobacter* with ammonia-nitrogen according to Burk and Horner (1935). We might also here recall the promoting influence of molybdenum on sugar consumption by strain 3 in nitrogen-deficient medium and hydrogen atmosphere, as discussed previously.

GENERAL CONCLUSIONS.

The experimental results show quite clearly that although molybdenum and vanadium have some influence on the general metabolism of the clostridia, their effect consists pre-eminently in an acceleration of the nitrogen-fixation process, as in *Azotobacter*. It is reasonable to assume that both kinds of bacteria may possess a nitrogen-fixing enzyme ("nitrogenase") that requires molybdenum as an activator, with vanadium as a less effective substitute; a certain difference in the enzymes seems to exist, in so far as in some of the clostridia they are not activated by vanadium.

Naturally the question then arises whether the biochemical processes of nitrogen fixation are fundamentally the same in the two groups of non-symbiotic nitrogen-fixing bacteria and perhaps in all cases of biological nitrogen fixation. At the present stage this can only be a matter for conjecture, but the fact that molybdenum, and often vanadium, but apparently no other elements, catalyze nitrogen fixation in types of life so different as *Azotobacter, Clostridium butyricum,* the *Azotomonas insolita* of Stapp (1940), the blue-green algae (Bortels, 1940) and the association of leguminous plants and root-nodule bacteria (e.g., Jensen, 1946), certainly speaks in favour of such a unitarian concept. For verification of this hypothesis, it would, among other things, be of great value to investigate the effect of molybdenum in certain other still incompletely known or problematical agents of biological nitrogen fixation, such as the mycorrhizal fungi (*Phoma* spp.) of the Ericaceae (Ternetz, 1907; Jones and Smith, 1928), the actinomycetes from the root nodules of *Alnus* spp. (von Plotho, 1940–41), and the practically unknown root-nodule organisms of *Casuarina* spp. in which there can be little doubt about the power of nitrogen fixation (Mowry, 1933).

SUMMARY.

Nine strains of *Clostridium butyricum* and one of *Cl. acetobutylicum* were tested for nitrogen-fixing power in a medium deficient in molybdenum but containing the necessary organic growth-compounds. All strains fixed small amounts of nitrogen in the basal medium, but the fixation was strongly increased, mostly three- to sixfold, by addition of small quantities of sodium molybdate. The yield of fixed nitrogen often exceeded three mgm. per gm. fermented glucose when adequate supplies of molybdenum were given.

A molybdenum-concentration of 0·01 part per million was nearly optimal, and the influence of 0·002 p.p.m. was still considerable. The effect of molybdenum appeared to begin at a concentration near or somewhat above $0·5 \times 10^{-8}$ molar.

In five strains of *Cl. butyricum*, molybdenum could be replaced by vanadium, which at higher concentration mostly gave an increase of nitrogen fixation equal to one-half to two-thirds of that caused by molybdenum, but which still showed some activity at a concentration of $0·4 \times 10^{-8}$ molar. Molybdenum could not be replaced by iron, manganese, zinc, cobalt, copper, niobium, tantalum, bismuth, chromium, uranium, or (probably) tungsten.

Molybdenum had only a relatively small or no stimulating effect on the rate of sugar fermentation with combined nitrogen (ammonia). It thus appears that molybdenum, partly replaceable by vanadium, is a specific catalyst of nitrogen fixation in *Cl. butyricum* as well as in *Azotobacter* and probably in other nitrogen-fixing forms of life.

REFERENCES.

BIRCH-HIRSCHFELD, LUISE, 1932.—Ueber den Einfluss von Molybdän und Bodenekstraktstoffen auf die N-Bindung von *Azotobacter chroococcum*. *Arch. Mikrobiol.*, 3 : 341-361.

BORTELS, H., 1930.—Molybdän als Katalysator bei der biologischen Stickstoffbindung. *Ibid.*, 1 : 333-342.

————, 1933.—Kurze Notiz über die Katalyse der organischen Stickstoffbindung. *Cent. Bakt.*, II, 87 : 476-477.

————, 1936.—Weitere Untersuchungen über die Bedeutung von Molybdän, Vanadium, Wolfram und andere Erdaschenstoffen für die stickstoffbindende und andere Mikroorganismen. *Ibid.*, II, 95 : 193-217.

————, 1940.—Ueber die Bedeutung des Molybdäns für stickstoffbindende Nostocaceen. *Arch. Mikrobiol.*, 11 : 155-186. Abstr. in *Biol. Abstr.*, 1941, 15 : 1385. (Original article not seen.)

BREDEMANN, G., 1909a.—Untersuchungen über die Variation und das Stickstoffbindungsvermögen des *Bacillus asterosporus* A. M. (etc.). *Cent. Bakt.*, II, 22 : 44-89.

————, 1909b.—*Bacillus amylobacter* A. M. et Bredemann in morphologischer, physiologischer und systematischer Beziehung. *Ibid.*, 23 : 385-568.

BURK, D., and HORNER, C. K., 1935.—The Specific Catalytic Role of Molybdenum and Vanadium in Nitrogen Fixation and Amide Utilization by *Azotobacter*. *Trans. 3rd Int. Congr. Soil Sci.* (Oxford), 1 : 152-155.

HORNER, C. K., BURK, D., ALLISON, F. E., and SHERMAN, M. S., 1942.—Nitrogen Fixation by *Azotobacter* as Influenced by Molybdenum and Vanadium. *J. Agric. Res.*, 65 : 173-192.

————, and ALLISON, E. F., 1944.—Utilization of Fixed Nitrogen by *Azotobacter* and Influence on Nitrogen Fixation. *J. Bact.*, 47 : 1-14.

JENSEN, H. L., 1941.—Nitrogen Fixation and Cellulose Decomposition by Soil Micro-organisms. iii. *Proc. Linn. Soc. N.S.W.*, 66 : 239-249.

————, 1946.—Nitrogen Fixation in Leguminous Plants. vi. *Ibid.*, 70 : 203-210.

JONES, W. N., and SMITH. M. L., 1928.—On the Fixation of Atmospheric Nitrogen by *Phoma radicis callunae* (etc.). *Brit. J. Exp. Biol.*, 6 : 167-189.

KLUYVER, A. J., and VAN REENEN, W. J., 1933.—Ueber *Azotobacter agilis* Beijerinck. *Arch. Mikrobiol.*, 4 : 280-300.

KOSTYTCHEV, S., 1924.—Chemical Plant Physiology. The Conditions and Quantitative Side of Nitrogen Fixation. (English Translation, 1931.)

KRZEMIENIEWSKI, S., 1908.—Untersuchungen über *Azotobacter chroococcum* Beij. *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math. Nat., Année* 1908 : 929-1050.

LAMPEN, J. O., and PETERSON, W. H., 1943.—Growth Factor Requirements of Clostridia. *Arch. Biochem.*, 2 : 443-449.

LANTSCH. K., 1921.—*Bacillus amylobacter* A. M. et Bredemann und seine Beziehung zu den Kolloiden. *Cent. Bakt.*, II, 54 : 1-12.

LÖHNIS, MARIE P., 1930.—Can *Bacterium radicicola* assimilate Nitrogen in the Absence of the Host Plant? *Soil Sci.*, 29 : 37-57.

MCCOY, ELIZABETH. HIGBY. W. M., and FRED, E. B., 1928.—The Assimilation of Nitrogen by Pure Cultures of *Clostridium Pasteurianum* and Related Organisms. *Cent. Bakt.*, II, 76 : 314-320.

————, FRED, E. B., and HASTINGS, E. J., 1930.—A Cultural Study of Certain Anaerobic Butyric-acid-forming Bacteria. *J. Inf. Dis.*, 46 : 118-137.

MOWRY, H., 1933.—Symbiotic Nitrogen Fixation in the Genus *Casuarina. Soil Sci.*, 36 : 409-425.

OMELIANSKY, V., 1916.—Sur la physiologie et la biologie des bactéries fixant l'azote. *Arch. Sci. Biol.*, 19 : 209-227. Abstr. in *Bull. Inst. Pasteur*, 1917, 15 : 133-134. (Original article not seen.)

OXFORD, A. E., LAMPEN, J. O., and PETERSON, W. H., 1940.—Growth Factor and Other Requirements of the Acetone-butanol Organism, *Cl. acetobutylicum. Biochem. J.*, 34 : 1584-1597.

VON PLOTHO, O., 1940.—Beiträge zur Kenntnis der Morphologie und Physiologie der Aktinomyzeten. *Arch. Mikrobiol.*, 11 : 3-72.

————, 1941.—Die Synthese der Knöllchen an den Wurzeln der Erle. *Ibid.*, 12 : 1-14.

PRINGSHEIM, H., 1908.—Ueber die Verwendung verschiedener Energiequellen zur Assimilation des Luftstickstoffs (etc.). *Cent. Bakt.*, II, 20 : 248-256.

————, 1910.—Weiteres über die Verwendung von Cellulose als Energiequelle zur Assimilation des Luftstickstoffs. *Ibid.*, 26 : 222-226.

RUBBO, S. D., MAXWELL, MARGARET, FAIRBRIDGE, R. A., and GILLESPIE, J. M., 1941.—The Bacteriology, Growth Factor Requirements and Fermentation Reactions of *Clostridium acetobutylicum* (Weizmann). *Aust. J. Exp. Biol.*, 19 : 185-198.

SJOLANDER, N. O., and MCCOY, ELIZABETH, 1937.—Studies on Anaerobic Bacteria. xiii. *Cent. Bakt.*, II, 97 : 314-324.

STAPP, C., 1940.—*Azotomonas insolita*, ein neuer aerober stickstoffbindender Mikroorganismus. *Ibid.*, II, 102 : 1-19. Abstr. in *Biol. Abstr.*, 1942, 16 : 420. (Original article not seen.)

TERNETZ, CHARLOTTE, 1907.—Ueber die Assimilation des atmosphärischen Stickstoffs durch Pilze. *Jahrb. wiss. Bot.*, 44 : 353-408.

WILLIS, W. H., 1934.—The Metabolism of Some Nitrogen-fixing Clostridia. *Iowa Agric. Exp. Stat. Res. Bull.* No. 173.

WILSON, P. W., HULL, J. F., and BURRIS, R. H., 1943.—Competition between Free and Combined Nitrogen in Nutrition of *Azotobacter. Proc. Nat. Acad. Sci. Wash.*, 29 : 289-294.

WINOGRADSKY, S., 1895.—Recherches sur l'assimilation de l'azote libre de l'atmosphère par les microbes. *Arch. Sci. Biol.*, 3 : 297-352.

WOOLLEY, D. W., MCDANIEL, L. C., and PETERSON, W. H., 1939.—Growth Factors for Bacteria. *J. Biol. Chem.*, 131 : 381-385.

EXPLANATION OF PLATE VII.

Cultures of clostridia in 50 ml. of Winogradsky's solution.

1.—*Strain 1*, inc. 14 d. 30°C. (Table 2, I) ; from left : 10 p.p.m. Na$_2$MoO$_4$—Control—Sterile medium.

2.—*Strain 1*, inc. 14 d. 30°C. (Table 2, IV) ; from left : 10 p.p.m. Na$_2$MoO$_4$—1·5 p.p.m. VOSO$_4$—Control.

3.—*Strain W*, inc. 14 d. 30°C. (Table 2, XIII) ; from left : 10 p.p.m. Na$_2$MoO$_4$—4 p.p.m. NH$_4$VO$_3$—Control.

(S. Woodward-Smith photos.)
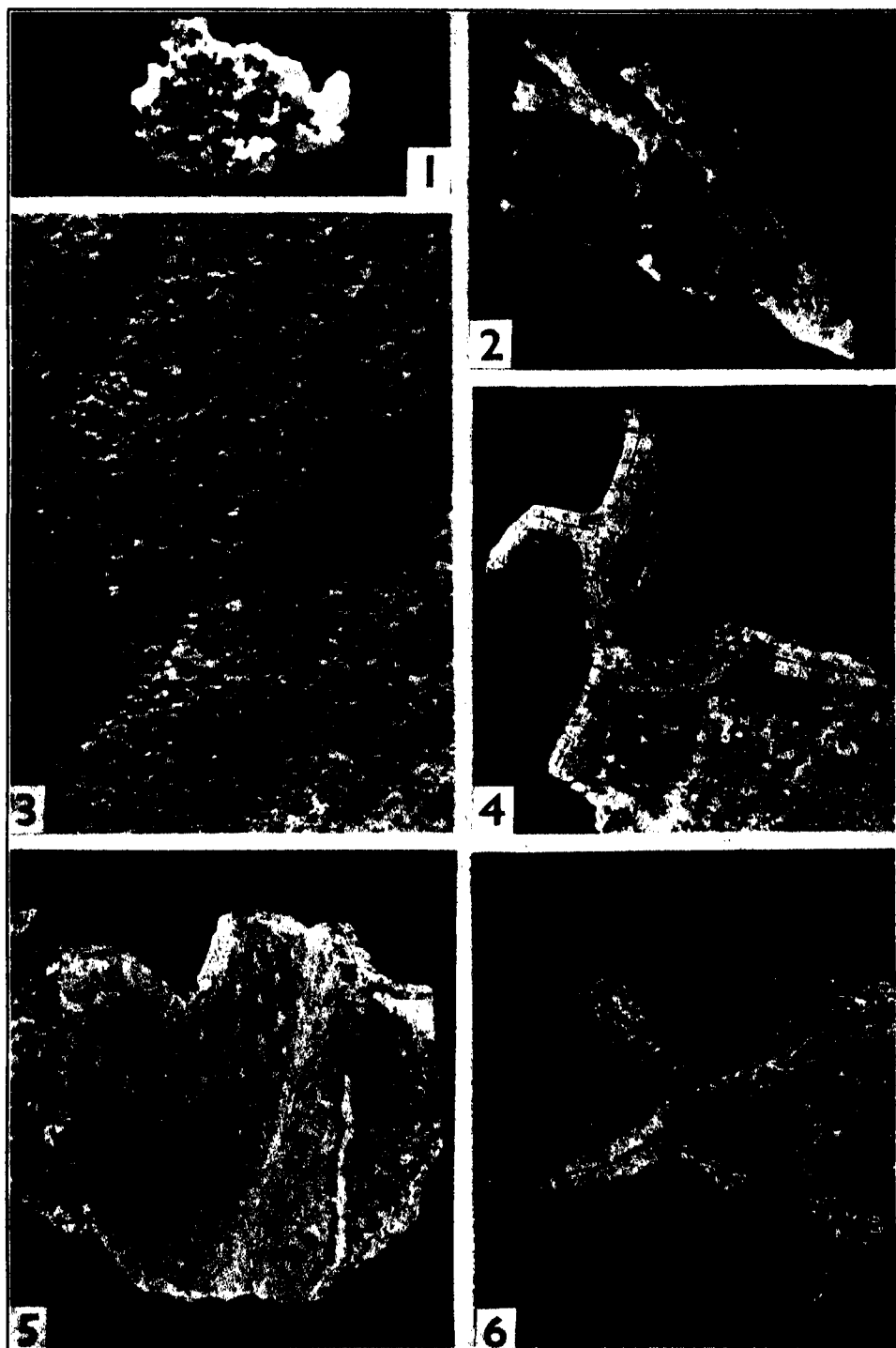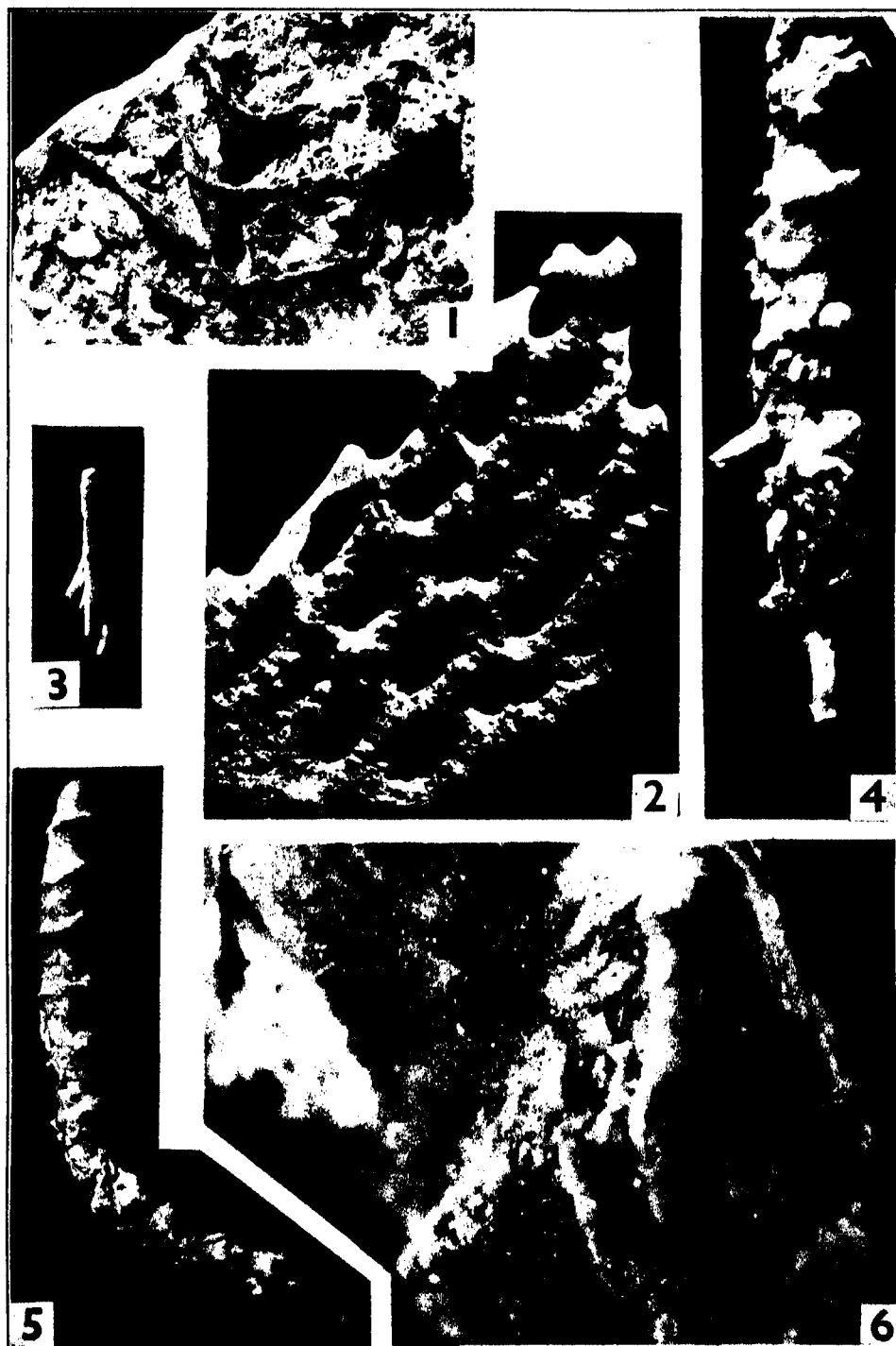
PLATE I.

Bryozoa from the Lower Carboniferous.

Bryozoa from the Lower Carboniferous.

Bryozoa from the Lower Carboniferous.

Bryozoa from the Lower Carboniferous.

Bryozoa from the Lower Carboniferous.

Bryozoa from the Lower Carboniferous.

`

PLATE VII.
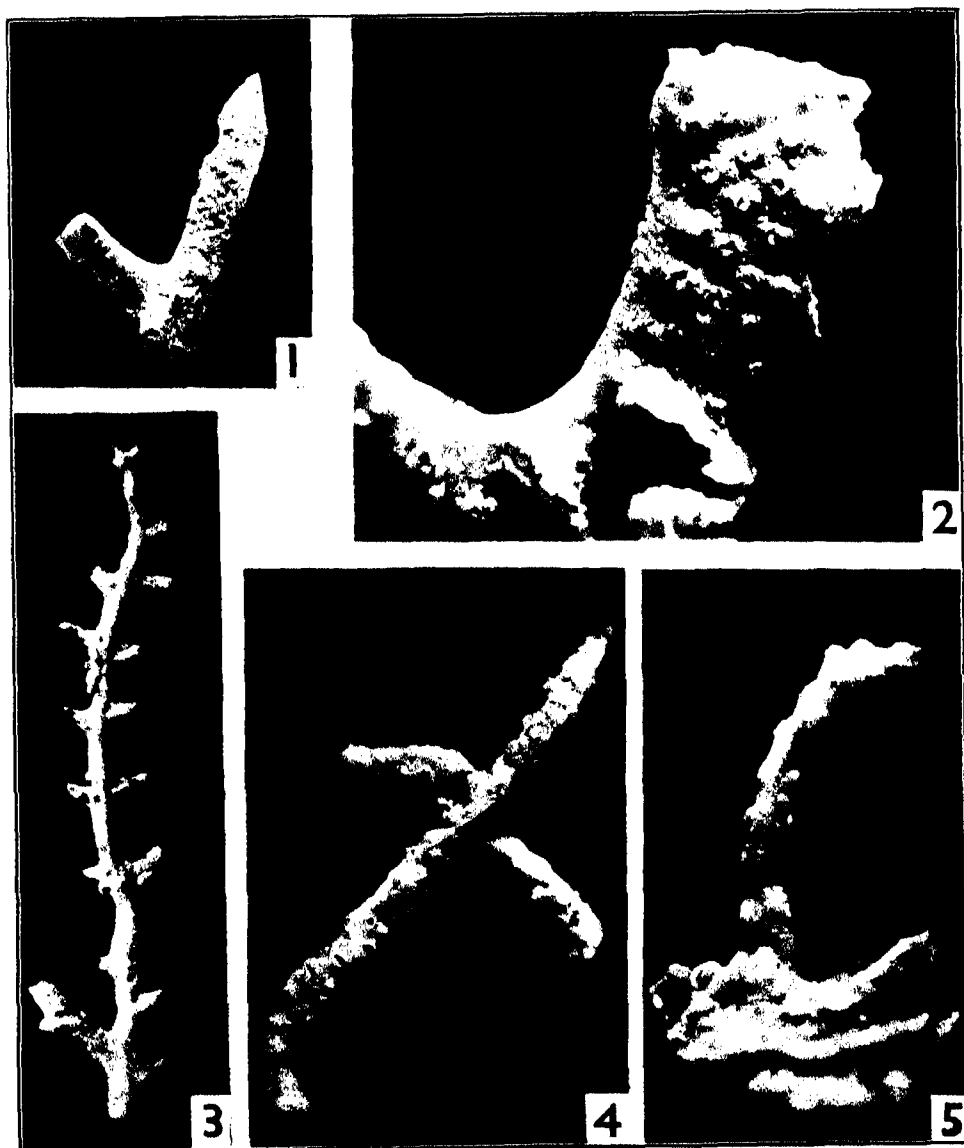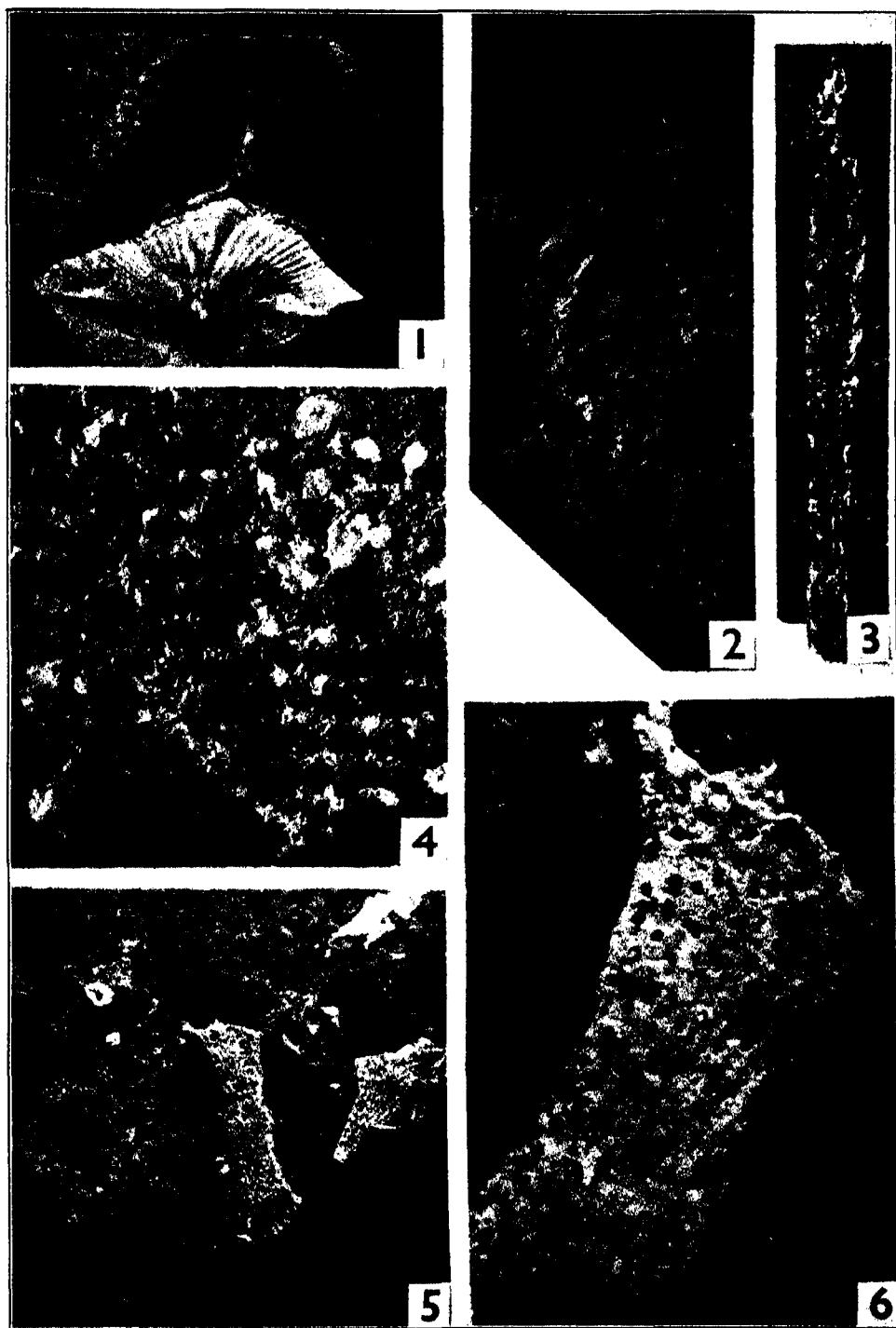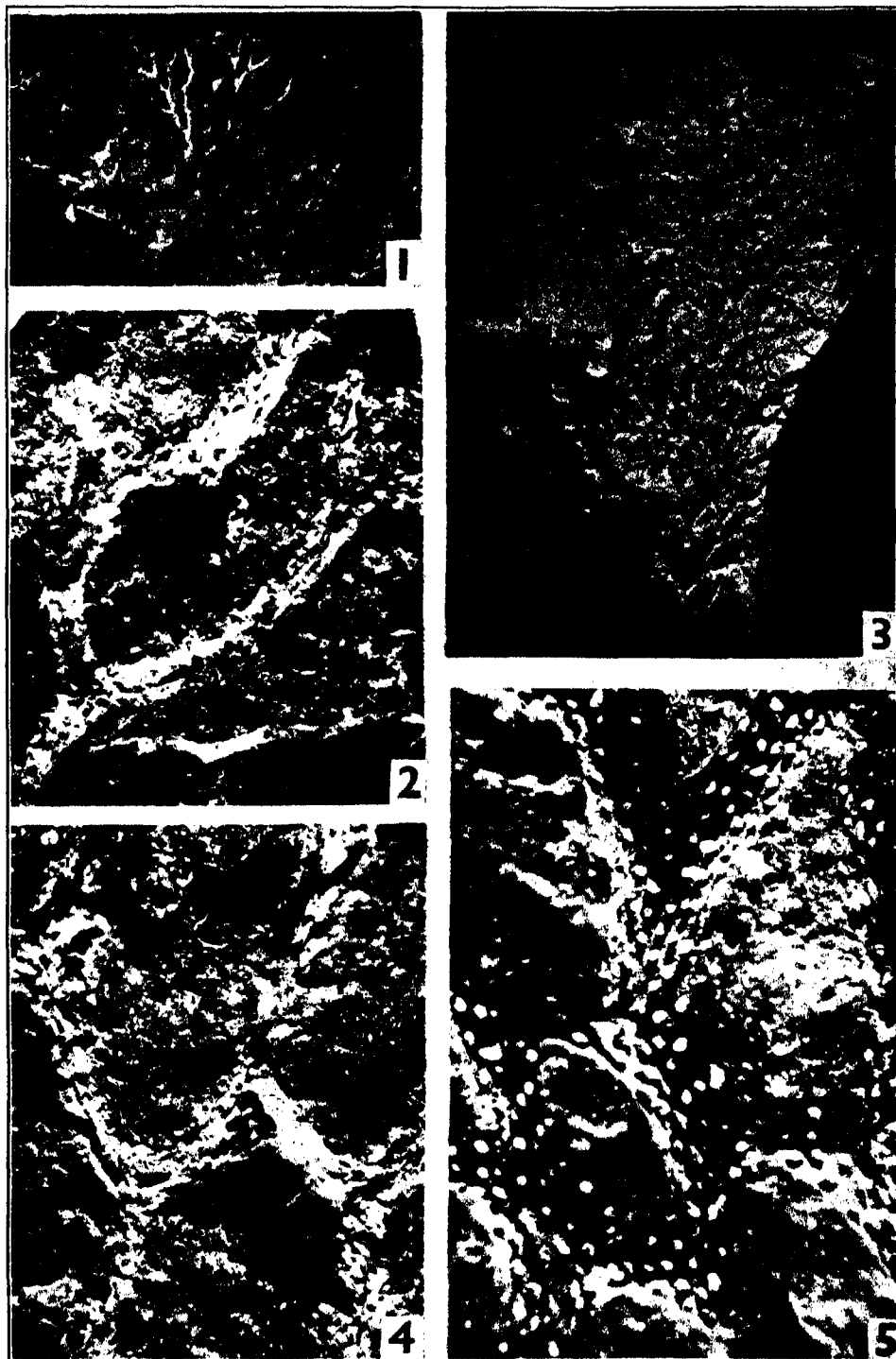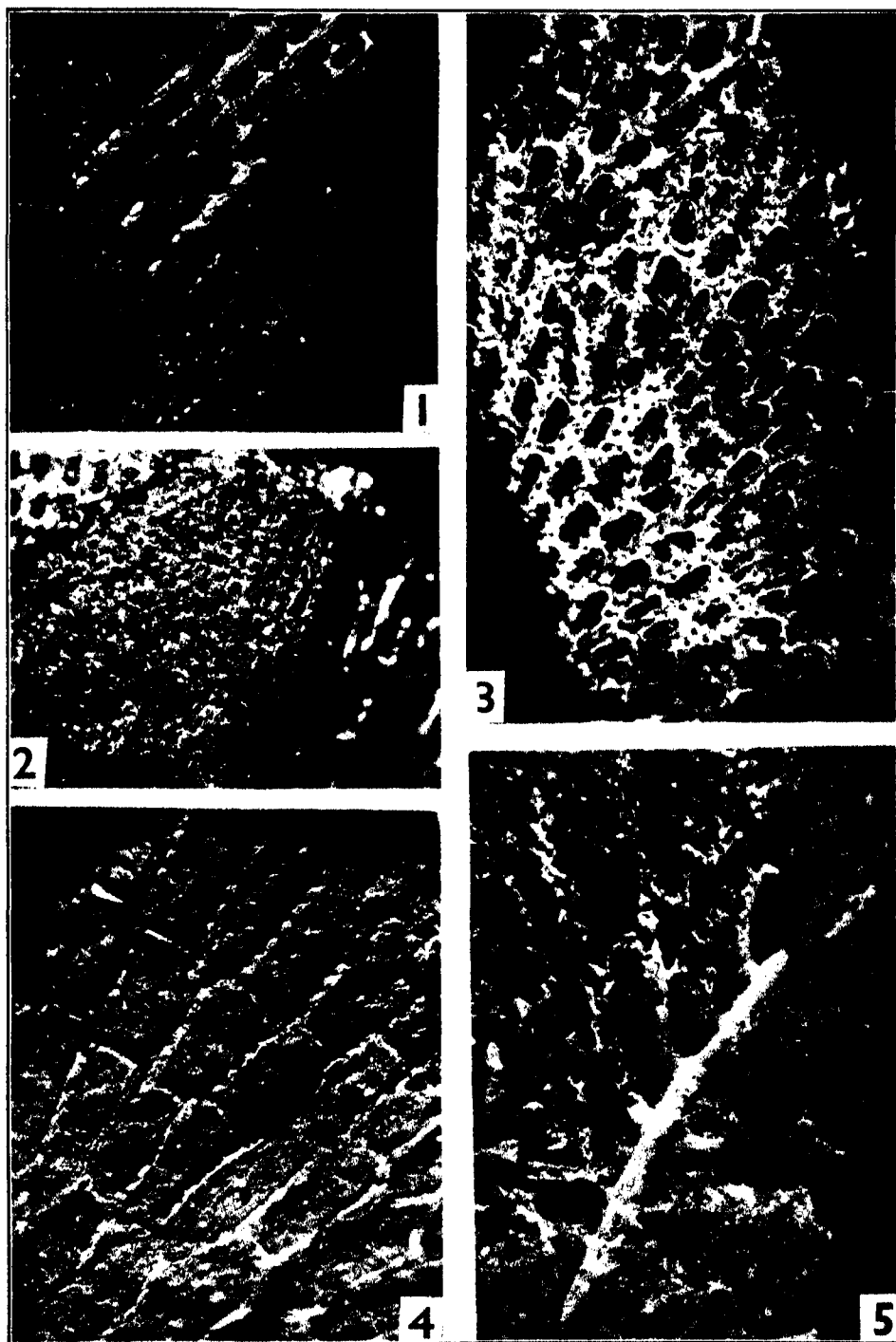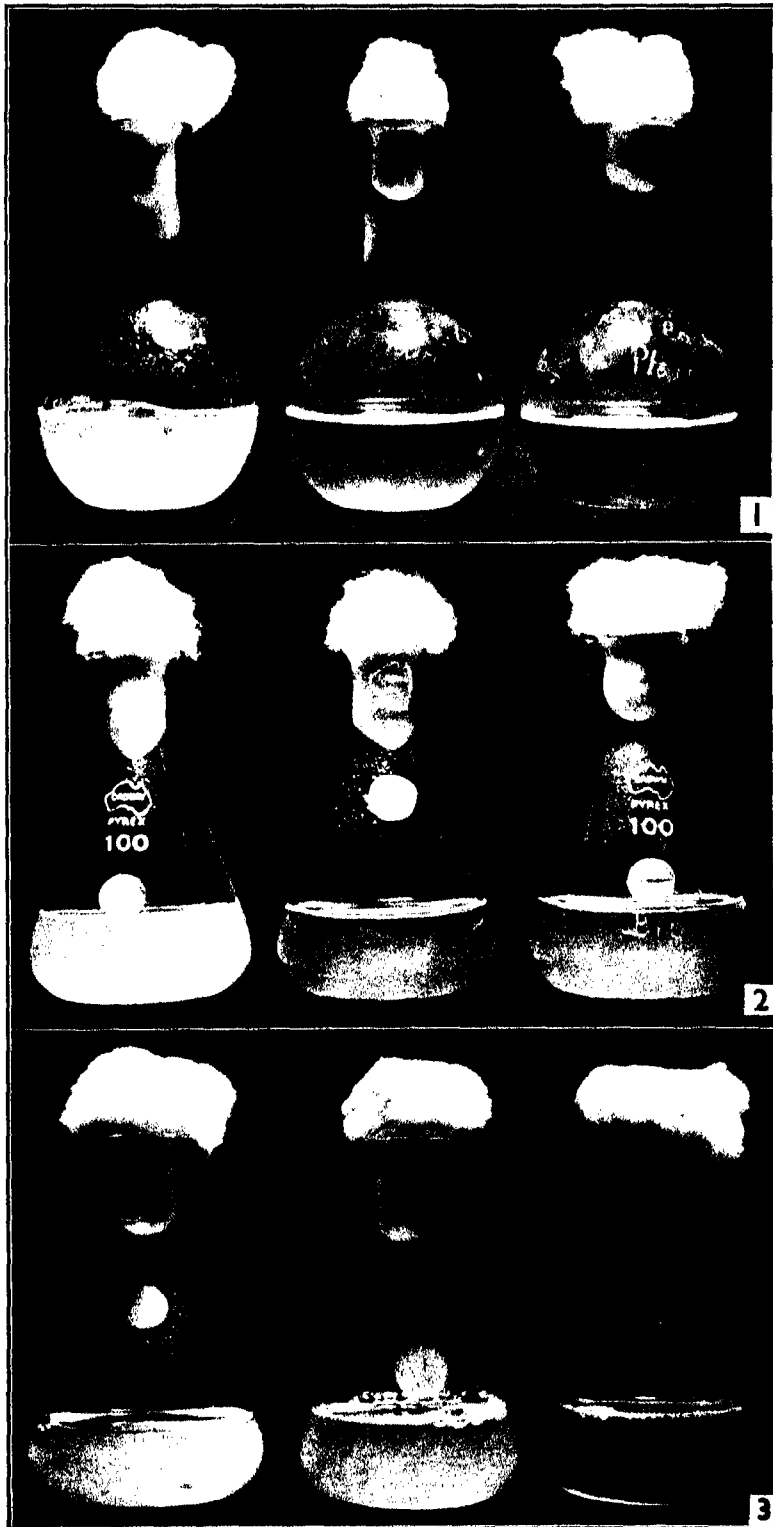
Nitrogen Fixation by *Clostridium butyricum.*

PETROLOGICAL STUDIES IN THE ORDOVICIAN OF NEW SOUTH WALES. IV.*

THE NORTHERN EXTENSION OF THE NORTH-EAST VICTORIAN METAMORPHIC COMPLEX.

By GERMAINE A. JOPLIN, B.Sc., Ph.D., Department of Geology, University of Sydney.†

(Plate xv; ten Text-figures.)

[Read 30th July, 1947.]

Contents.

I. INTRODUCTION.

As implied by the title of this paper, the area under consideration is an extension of the great Victorian Metamorphic Complex, and although a good deal of petrographical work has been done on the Victorian rocks, it is not quite detailed enough to make possible the placing of the New South Wales types in the general metamorphic pattern; thus certain assumptions are made, which may prove incorrect when a more detailed study is made of the complex as a whole on the southern side of the Murray River.

Recently the writer (1944) published a brief account of the geology of the Albury district, and although subsequent more detailed work shows that slight modifications are necessary, the present paper is partly a petrological elaboration of that area together with a rather more generalized description of the country in the vicinity of Woomargama and Jingellic. The region examined has an area of approximately 800 square miles and represents work in varying degrees of detail (see Plate xv). It is hoped, however, that it gives a fairly reliable general picture of the metamorphism and of the various granite intrusions that have from time to time invaded this complicated area.

II. THE COUNTRY ROCKS.

1. NATURE OF THE ORIGINAL COUNTRY ROCKS.

(a). Sedimentary Types.

In the areas of less altered rocks about Jingellic, excellent sections of the sediments are exposed. Certain parts of the Holbrook Road, several miles east of Lankey's Creek Post Office, cut obliquely across the strike of a great series of comparatively

---

H

narrow alternating beds of light grey, buff and black pelites and psammites. In places, the sandy type is the more prominent, in other parts, it is almost absent, and the beds, though still fairly narrow, and rarely exceeding 18″ in thickness, show alternations of black and grey pelite. Close examination shows that many of the pelites are somewhat sandy types and should be termed more correctly psammopelites.

In areas of greater metamorphism the same rock-types may be recognized among the high-grade schists, and chemical analyses show that the pelites are normal or aluminous pelites as defined by the present writer (1942). The siliceous pelites met with at Cooma (Joplin, 1942) and elsewhere in the Ordovician of New South Wales (Joplin, 1945) have not been observed in the Murray Valley; although a few rocks are more siliceous than the normal pelites, their high alumina content shows them to be variations of that group. Reference to Tables 1, 2 and 3 will show other variations from the normal as well. Thus a number of rocks (Table 2) contain lower magnesia

TABLE 1.
Normal Pelites.

		I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.
SiO_2	.. ..	55·49	56·52	56·33	50·42	51·33	54·18	58·87	56·40	54·63	56·05	59·05
Al_2O_3	.. ..	24·45	23·13	22·94	21·44	25·60	25·48	21·23	23·20	25·35	24·91	22·95
Fe_2O_3	.. ..	2·21	1·96	2·19	1·09	4·80	2·99	2·47	1·30	2·40	1·22	1·48
FeO	.. ..	4·92	5·09	4·54	5·23	1·07	3·08	4·05	5·22	4·64	4·76	5·16
MgO	.. ..	2·88	2·82	3·27	2·53	2·72	3·13	2·98	3·24	2·75	2·51	2·37
CaO	.. ..	0·35	0·39	0·25	0·11	0·25	0·41	0·12	0·63	0·65	0·51	0·65
Na_2O	.. ..	0·54	0·24	0·88	0·66	0·77	0·73	0·60	0·61	0·62	1·06	0·81
K_2O	.. ..	5·21	6·14	6·10	6·14	6·13	5·70	5·73	5·65	6·28	6·12	5·85
$H_2O +$	.. ..	2·09	2·27	3·07	1·82	5·20	2·88	2·59	2·77	1·25	1·23	1·17
$H_2O -$	.. ..	0·07	0·20	0·80	0·19	1·53	0·48	0·22	0·30	0·26	0·22	0·18
TiO_2	.. ..	0·78	1·17	—	0·96	0·49	0·73	0·84	0·57	0·86	0·86	0·68
P_2O_5	.. ..	0·20	0·22	0·13	0·04	—	0·07	0·05	0·06	0·20	0·14	0·18
MnO	.. ..	0·09	0·06	tr.	0·05	—	0·03	0·02	0·01	0·05	0·11	0·05
ZrO_2	.. ..	n.d.	—	--	n.d.	—	n.d.	0·02	0·05	0·15	0·09	0·19
C	.. ..	0·03	---	---	—	---	0·34	0·16	0·51	—	---	—
CO_2	.. ..	0·30	—	—	abs.	—	abs.	abs.	abs.	abs.	abs.	abs.
BaO	.. ..	—	0·11	---	—	—	—	—	—	—	—	—
		99·61	100·32	100·50	99·68	99·98	100·23	99·95	100·52	100·09	99·79	99·86

I. Knotted Schist. Just NW. of Hamilton Trigonometrical Station, Por. 275, Par. of Jindera, Albury. Anal. G. A. Joplin.

II. Andalusite Hornfels. Noorongong. Anal. C. M. Tattam. *Geol. Surv. Vict.*, Bull. 52, 1929 : 35.

III. Phyllite. Ensay Area. Anal. W. A. Howitt. *Proc. Roy. Soc. Vict.*, 22, 1886 : 68.

IV. Permeation Gneiss. Eastern Hills, Pors. 107/74, Par. of Albury. Anal. G. A. Joplin.

V. Argillite. Waterford, Dargo Road and Mitchell River Crossing. Anal. A. W. Howitt. Ibid., 23, 1887 : 130.

VI. Chlorite-sericite-schist. About half a mile east of McCarthy's Crossing, Por. 144, Par. of Coolrington. Anal. G. A. Joplin. PROC. LINN. SOC. N.S.W., 67, 1942: 181.

VII. Plicated Mica-schist. Crossing of Slack's Creek and Dry Plain Road. Anal. G. A. Joplin. Ibid.

VIII. Knotted Andalusite-schist. Por. 137, Par. of Binjura. Anal. G. A. Joplin. Ibid.

IX. Spotted Granulite. Por. 212, Par. of Binjura. Anal. G. A. Joplin. Ibid.

X. Mottled Gneiss. Spring Creek. Por. 212, Par. of Binjura. Anal. G. A. Joplin. Ibid.

XI. Mottled Gneiss. Same locality as X. Anal. G. A. Joplin. Ibid.

than that characteristic of the normal types, and these, as well as the more normal and more siliceous pelites (Tables 1 and 3), show variations in soda and in total iron. Nevertheless, these discrepancies are not so great as to warrant the assumption that these sediments had a markedly different origin.

In Tables 1–3 analyses of the Albury–Jingellic pelites are grouped with rocks from various parts of the Victorian Complex, thus indicating that these types of sediment are widespread and form the dominant country-rock within the entire complex. Furthermore, with reference to the Victorian region, Howitt (1889) comments upon "the characteristic alternations of argillaceous and arenaceous beds"—a feature particularly noticeable in the Jingellic area, as mentioned above.

Although no graptolites have been found in the Albury–Jingellic area, the rocks have been traced into Upper Ordovician graptolite-bearing types by Howitt (1884) and

by Tattam (1929), and in view of the close lithological and chemical similarities between these rocks and those of Cooma, they are regarded as Ordovician sediments, probably to be correlated with the Binjura Beds of the Cooma district.

TABLE 2.

Magnesia Content lower than that of the Normal Pelites.

	I.	II.	III.	IV.
SiO₂	53·88	57·74	59·43	52·91
Al₂O₃	27·95	23·06	23·37	24·49
Fe₂O₃	5·04	2·90	2·84	5·45
FeO	0·69	1·61	1·13	1·50
MgO	1·02	1·97	1·59	1·80
CaO	0·19	0·14	0·14	0·29
Na₂O	0·34	0·46	0·61	1·08
K₂O	5·64	5·38	5·09	6·60
H₂O + ...	3·44	3·76	2·48	3·81
H₂O −	0·72	1·03	0·61	0·61
TiO₂	1·12	0·92	0·98	0·83
P₂O₅	0·07	0·10	tr.	0·10
MnO	0·03	0·04	0·01	0·06
BaO	—	—	—	0·06
C	0·53	0·87	1·75	0·19
	100·66	99·98	100·03	99·78

I. Dark Grey Slate. Tumbarumba Road, 3 miles from Jingellic, Por. 12, Par. of Currajong. Anal. G. A. Joplin.

II. Spotted Black Slate. Near Abraham's Bosom, roadside cutting, Por. 23, Par. of Talmalmo. Anal. G. A. Joplin.

III. Dark Grey Slate. Holbrook Road, Por. 55, Par. of Currajong. Anal. G. A. Joplin.

IV. Slate. Eastern slopes of Mt. Wagra, near Tallangatta. Anal. C. M. Tattam. *Geol. Surv. Vict.*, Bull. 52, 1929.

TABLE 3.

Silica Percentage higher than that of Normal Pelites, also Alkalis and Total Iron somewhat Irregular. Analysis I contains Lower Magnesia.

	I.	II.	III.	IV.	V.	VI.
SiO₂	65·73	64·00	62·28	62·30	61·92	61·13
Al₂O₃	21·04	19·82	20·16	19·22	20·74	23·43
Fe₂O₃ }	2·28	3·50	{ 0·53	1·80	2·28	0·09
FeO }			3·84	4·01	3·90	4·84
MgO	0·75	2·14	2·54	2·95	2·19	1·99
CaO	0·14	0·32	0·82	0·44	0·42	0·63
Na₂O	0·27	1·10	1·29	2·07	3·51	1·08
K₂O	4·77	4·41	6·40	3·60	2·28	5·84
H₂O + ...	2·57	1·38	1·14	1·96	1·20	0·26
H₂O −	0·25	0·85	0·72	0·40	0·92	0·20
TiO₂	0·92	—	0·17	—	—	0·72
P₂O₅	0·08	0·10	0·15	0·23	0·16	0·24
MnO	—	—	—	—	0·17	0·09
C	1·59	3·32	—	—	—	—
ZrO₂	—	—	—	—	—	0·16
	100·39	100·94	100·04	98·98	99·69	100·70

I. Carbonaceous Sericite Schist, slightly hornfelsed. Por. 16, Par. of Burrumbuttock. Anal. G. A. Joplin.

II. Mica-schist. Wilson's Creek, Omeo Area. Anal. A. W. Howitt. *Trans. Roy. Soc. Vict.*, 24, 1887: 112.

III. Hornfels. Orr's Gully, Dargo Area. Anal. A. W. Howitt. Ibid., 23: 133.

IV. Slate. Junction Haunted Stream and Tambo River. Ibid., 20, 1884: 58.

V. Hornfels. Above Locality. Anal. A. W. Howitt. Ibid., 62.

VI. Mottled Gneiss. Mt. Gladstone, Cooma, Por. 145, Par. of Jillamatong. Anal. G. A. Joplin. Proc. Linn. Soc. N.S.W., 67, 1942.

(b). *Rocks of Igneous Origin.*

Near Bethanga Bridge, just to the west of the Hume Weir Quarry, a mass of basic igneous rock occurs associated with the granite. The relation of the two rocks is rather obscure and it may represent a later intrusion into the granite or part of the country-rock occurring as a roof-pendant. In thin section the basic type shows a good deal of alteration, but does not appear to be in a high grade of metamorphism like the numerous pyroxene-granulite xenoliths found in the Bethanga gneiss within the quarry itself. Numerous blocks of quarried gneiss and granite contain this lower-grade type, however, and one of these was analysed and compared with an analysis of a granulite xenolith. It will be seen in Table 4 that the two rocks are comparable, though by no means identical, and the question of their relationship must be deferred until further field evidence becomes available. Reference to Table 4 shows also that these rocks appear to be of the same magma-type as certain hornblende and pyroxene granulites from Cooma, which, it was suggested (Joplin, 1942), represented basaltic flows or sills within the Binjura Beds.

TABLE 4.

	I.	II.	III.	IV.	V.
SiO$_2$	52·23	48·23	49·50	47·24	47·26
Al$_2$O$_3$	22·16	16·67	16·42	18·55	22·80
Fe$_2$O$_3$	0·72	2·66	0·72	6·02	2·21
FeO	8·50	6·09	9·10	4·06	5·41
MgO	4·75	7·65	7·47	5·24	7·76
CaO	7·29	9·22	14·79	11·72	10·93
Na$_2$O	0·43	1·67	0·47	2·42	1·72
K$_2$O	1·70	0·84	0·32	0·15	0·20
H$_2$O +	0·73	3·17	0·57	2·24	0·90
H$_2$O -	0·01	0·25	0·03	0·21	0·11
TiO$_2$	0·76	0·78	0·75	1·46	0·38
P$_2$O$_5$	0·46	0·26	0·05	0·26	0·06
MnO	0·11	0·15	0·16	0·31	0·31
CO$_2$	abs.	1·88	abs.	—	—
Etc.	—	—	—	0·24	0·10
	99·85	99·52	100·35	100·12	100·24
Sp. Gr.	2·83	2·81	—	—	—

I. Pyroxene-granulite. Large inclusion in Bethanga Gneiss. Weir Quarry, Por. 65, Par. of Thurgona. Anal. G. A. Joplin.

II. Altered Basic Rock. Road cutting between turn-off to Hume Weir and Bethanga Bridge. Pors. 66/67, Par. of Thurgona. Anal. G. A. Joplin.

III. Hornblende-granulite (with trace of pyroxene). Cooma Creek, near entrance to gorge, Por. 135, Par. of Cooma. Anal. G. A. Joplin. PROC. LINN. SOC. N.S.W., 67, 1942 : 172.

IV. Basalt (porphyritic central type) Tertiary lava. ½ mile SSW. of Derrynaculen, Mull. Anal. E. G. Radley. *Mem. Geol. Surv. Scot.*, 1924 : 24.

V. Biotite-eucrite. Ring-dyke Centre 3, Ardnamurchan. Bank of stream 1 mile east 33 south of Achnaha. Anal. E. G. Radley. Ibid., 1930 : 85.

The pyroxene granulites and certain related types, which are believed to represent admixtures of basic tuff and normal sediments, are described in detail in connection with the xenoliths in the cordierite-bearing gneiss (see p. 100).

2. THE METAMORPHIC ZONES.

In the Cooma district the metamorphic zones could be mapped fairly accurately, and it was shown that granitized areas, consisting of injection- and permeation-zones, surrounded the main mass of Ordovician gneiss. These were followed outwards by a zone of piezo-contact metamorphism, termed the andalusite-zone, and this again by biotite- and chlorite-zones. It was established that the granitized schists and andalusite-schists were formed directly as a result of the intrusion of the Ordovician gneiss, and although it was surmised that the biotite- and probably the chlorite-zones bore a causal relation, this point could not be verified owing to the paucity of outcrops.

In the Albury–Jingellic area the zones are not well defined and cannot be strictly correlated with those of Cooma since the Albury area represents only the northern periphery of the main complex of Victoria, and it is possible that this represents a different level of the intrusion from that of Cooma. Moreover, in the Murray Valley, the metamorphic pattern is obscured by intrusions of later granites, and many of these have superimposed hornfels-zones on the Ordovician schists.

The Albury district shows a conspicuous development of sills in the vicinity of the gneisses, and although these have been responsible for granitizing and sometimes felspathizing the schists, their margins are usually well defined and they do not give rise to injection-gneiss. Actually, a little very localized injection is to be seen within the zone of sills, as on the western shore of the Bowna Arm of the Hume Reservoir, and in several road sections within the town. At the northern end of Eastern Hills, a large sill has been responsible for the permeation of the surrounding schists, which compare with the permeation or mottled gneisses of Cooma.

Along the Howlong Road, between West Albury and Bungowannah, the schists are high-grade types, often sillimanite gneisses. These are within the zone of sills and pass rapidly into knotted schists which are also partly within the zone of sills. No attempt has been made to map the junction between the sillimanite-zone and the zone of knotted schists, but the line of demarcation between the zone of sills and the outer part of the knotted schist zone, though not sharply defined in the field, is shown as a rough sketch boundary on the map (Plate xv).

North of Albury the knotted schists pass into biotite schists, and again, the boundary shown on the map is only approximate, but it is fairly obvious that all three zones run approximately east and west and are possibly marginal to a gneissic body south of the Murray, the northern margin of which crops out west of the town on the banks of the river and on the lower southern flank of Monument Hill.

Other smaller masses of gneiss with their corresponding zones are to be found in the Parish of Bowna on the shores of the northern arm of the reservoir, at Woomargama, and about 10 miles from Jingellic on the Tumbarumba Road in the Parish of Coppabella. There is also good reason for believing that a mass of gneiss, subsequently engulfed by later granite, occurred a few miles south-east of Jingellic, since by analogy with other areas of gneiss, outcrops of knotted schist on Horse Creek and on the banks of the Murray suggest the former presence of gneiss.

Thus, though the metamorphic zones are not so easy to trace as at Cooma, they appear to exist or to have existed before being stamped out by later metamorphic changes.

In examining the metamorphic rocks in the Omeo district which is situated near the southern end of the complex, Howitt (1889) has traced the progressive regional metamorphism of what were then considered to be Silurian rocks into highly-crystalline schists and gneisses. He describes the unaltered rocks as a series of interbedded arenaceous and argillaceous rocks, and calls rocks showing an early stage of alteration "argillites" (see Table 1, Anal. V). He speaks of these low-grade rocks as containing members of the chlorite group and recognizes this change as "one of the earliest stages of metamorphism impressed upon them (the beds) during the folding of the strata". At the next stage, he observes phyllitic characters developed and mentions that these pass into mica-schists and ultimately into massive holocrystalline rocks with the characters of quartz-diorites. Although Howitt did not map these stages as, or call them, metamorphic zones, he tacitly recognized them as such. This is of very great interest, for it was not until 1893 that Barrow put forward his ideas concerning the Highland zones, and it was in 1925 that Tilley suggested the use of chlorite as an index of low-grade argillaceous rocks.

Tattam (1929), in describing the Victorian Complex as a whole, makes no attempt to trace metamorphic zones, largely on account of retrograde effects. Nevertheless he mentions the occurrence of chloritic slates and phyllites at Tawonga Gap and on the divide between Twist's and Commissioner's Creeks, near Yackandandah (pp. 12 and 18).

As already explained, the present writer is attempting to compare the Murray Valley rocks with those of Cooma where metamorphic zoning is fairly simple, but to do this satisfactorily the Victorian rocks must also be considered. Obviously zoning is possible in the areas where Howitt has worked, but it is a little difficult to correlate Tattam's phyllites, injection schists and schistose phyllite with the various zones. I have been greatly assisted in this correlation by the kindness of Mr. Baragwanath, who has lent me a large collection of microscope slides from this region, and, so far as I can ascertain, Tattam's phyllites cover all types from the lowest grade up to the zone of knotted schists. He speaks of the occurrence of chlorite and of biotite in these rocks and describes some types containing oval knots in a two-mica base. His injection schists appear to be comparable to some of my high-grade altered schists and gneisses which occur within the zone of sills, and so far as I am able to tell, his schistose hornfelses are the more psammatic types within this same zone.

In the Albury–Jingellic region, later granites have superimposed their contact effects, and Tattam has recognized similar phenomena on Indigo Creek in the contact of the Pilot Range granite and further south in the Tambo River area. These rocks Tattam (1929, p. 18) describes as hornfelses.

3. PETROGRAPHY OF THE ORDOVICIAN SCHISTS.

(a). Schists of the Chlorite and Biotite Zones.

Low-grade rocks belonging to the chlorite-zone are developed in the vicinity of Talmalmo and Jingellic, but many have suffered a superimposed contact metamorphism near the margins of the younger granite intrusions (see p. 122).

In both these areas the pelitic type of sediment is more common than the psammatic, though the microscope reveals minute sandy bands in most of the pelitic rocks.

In handspecimen the rocks are grey or black slates with a fairly well-developed cleavage. Occasionally they are slightly phyllitic.

Under the microscope they are found to be slightly banded, and minute cross-cutting veins of quartz or of iron ore are not infrequent.

Chlorite, sericite and a little quartz are the main constituents, the latter being more abundant in the psammatic bands. In the darker rocks carbonaceous material is prominent. Accessory minerals are zircons and iron ore. Chlorite usually occurs in minute flakes in parallel orientation, but in some types larger flakes or plates, clouded with carbonaceous material, occur. The chlorite is optically negative and colourless to very pale green. The double refraction varies from nothing to 0·005. In the vicinity of the cross-cutting veins containing haematite, a little biotite or green mica may be developed, and in some slates darker micas are developed near haematite streaks which are parallel to the schistosity. Sericite occurs in flakes parallel to the schistosity or as minute blades piercing chlorite plates.

Biotite-schists occur north-west of Albury near Burrumbuttock, to the north-east near Woomargama and up the river near Jingellic. In many cases they have suffered a subsequent contact metamorphism.

The biotite-schists vary a good deal in handspecimen, some of the Jingellic types looking not unlike phyllitic slates and being indistinguishable from the slates of the chlorite-zone. North and north-west of Albury, however, they are usually coarser grained, and often mica may be distinguished in handspecimen. In this area, and also in the area about Woomargama, psammatic types are prominent, and these form typical quartz-mica-schists.

Under the microscope the pelites of the biotite-zone vary a good deal in texture and grain-size. Near Jingellic a fine-grained biotite-schist shows a slight development of false cleavage. There is a great development of minute flakes of greenish-brown mica parallel to the schistosity and small porphyroblasts of biotite are developed across it. Harker (1932, p. 215) considers this to be an early stage in the biotite-zone. The development of biotite in the vicinity of haematite is mentioned above in connection with the chlorite-zone and a specimen from Burrumbuttock, within the biotite-zone, shows a related feature. In this case an aureole of chlorite-sericite-schist surrounds

haematitized pyrites crystals in a rock which normally contains a good deal of greenish-brown mica.

At Burrumbuttock carbonaceous quartz-sericite-schists are fairly common, and though they contain no biotite, their well-marked plication and schistosity indicate that they probably belong to the biotite-zone, their initial composition inhibiting the production of the index mineral.

The biotite-schists are often finely banded with minute (0·5 mm.–3 mm.) seams of psammite alternating with pelite.

Lenses of biotite, or small porphyroblasts orientated with their basal cleavage at an angle of about 30° to the schistosity, may be developed in a fine lepidoblastic aggregate of biotite, sericite and quartz. The amount of biotite is variable and white mica may be poorly developed in some types.

Tourmalinitized biotite-schists have been collected from Por. 317, Parish of Moorwatha, and Por. 131, Parish of Mungabarina.

Psammopelites are fairly common in the areas where the biotite-zone is developed. These contain a greater proportion of quartz than the pelites, but the mineral constituents and structures are similar. The quartz usually occurs in small elliptical grains with their longer axes parallel to the schistosity.

About Burrumbuttock the most prominent rock-type is a fine-grained buff-coloured slate, which, on microscopic examination, proves to be an extremely fine-grained psammopelite containing quartz, greenish mica, biotite, some muscovite, iron ore and tourmaline. In some types small porphyroblasts of chlorite lie athwart the schistosity.

Unlike the psammites in the biotite-zone of Cooma, those of the Burrumbuttock and Woomargama districts show a well-preserved clastic structure. The clastic grains are usually quartz of varying size (1·0 mm.–0·1 mm.). These are somewhat lenticular and often granulated, but not infrequently occur in irregular grains across the schistosity. Undulose extinction is common, and cross-cracking and lines of minute inclusions at right angles to the incipient schistosity of the rock are often developed. The matrix consists of biotite, green mica, muscovite and quartz, whilst tourmaline and iron ores are often accessory. Detrital grains of sphene and of apatite occur. The former are sometimes recrystallized.

A rock east of Moorwatha Trig. shows clastic quartz grains with undulose extinction and a marginal development of secondary quartz. There is little evidence of regional metamorphism, and the rock appears to have been slightly hornfelsed, although no granite mass has been observed in the vicinity.

A rock from the roadside opposite the T.S.R., south of Woomargama, contains a small quantity of clastic plagioclase showing a clouding of minute black grains (Macgregor, 1931). The rock may represent an arkose or may contain a little original tuffaceous material. In the field it appears as a greenish-grey psammite.

(b). Zone of Knotted Schists.

The inner part of the zone of knotted schists lies within the zone of sills. All of the pelites and most of the psammopelites and psammites within this zone show a development of dark spots, which stand out as knots on weathered surfaces. The knots vary considerably in size from a few millimetres up to an inch (Fig. 1). The schists are distinctly micaceous and within the zone of sills mica is developed in very large flakes and the rock appears coarser than usual.

In thin section the spots may show a distinct zoning, which when examined more closely under the microscope is not so apparent. Sometimes the zoning is due to a difference in texture, sometimes to a concentration of carbonaceous material or to the development of biotite in the centre of the spot. Most of these areas are circular or elliptical in section and consist largely of green micaceous material exactly similar to the altered cordierite of the cordierite-bearing gneiss (see p. 107). Often the green mica shows a well-developed sieve structure. Chlorite, red-brown biotite and quartz are usually present as well, and sometimes white mica or a large quantity of carbonaceous material—probably finely-divided graphite. A rock from the track just west of Bungamba Trig. shows a zoned spot consisting of an inner core of bright orange, isotropic pinite

and an outer rim of green micaceous material. Both show well-developed sieve-structure. The presence of pinite suggests strongly that the original spot consisted of cordierite. Another rock from the Gap Road north of Hamilton Trig. contains large plates of green mica threaded with parallel bands of haematite around which wisps of biotite have developed. These seem to mark an original cleavage and suggest that the knot was originally andalusite. In the twenty-six microslides examined from this zone, no fresh cordierite or andalusite has been detected, but in slides kindly lent by Mr. W. Baragwanath from the head of Forest Creek, Talgarno, Victoria, both these minerals have been observed. These highly-plicated carbonaceous rocks from Victoria would appear to lie within the zone of knotted schists and outside the zone of sills. It is of interest to note that the analysis of a knotted schist from the Albury district compares closely with a knotted andalusite-schist, containing some cordierite, from Cooma, and with an andalusite hornfels described by Tattam (1929) from the Mitta Mitta Valley (Table 1). Furthermore, in a higher grade of metamorphism, andalusite and/or sillimanite and occasionally cordierite are developed in the Albury area.

Although no direct comparison can be made, it is of interest to examine three analyses carried out by Tattam. The first is a "chloritic" nodule from a knotted phyllite which would appear to correspond to the spots of the Albury knotted schists, and the others are analyses of pinitized cordierite.

TABLE 5.

			I.	II.	III.
SiO₂	..	..	50·01	45·73	44·92
Al₂O₃	..	..	23·15	27·83	27·30
Fe₂O₃	..	..	4·07	1·05	2·84
FeO	..	..	4·71	6·80	7·60
MgO	..	..	4·35	4·95	3·05
CaO	..	..	0·20	0·20	0·40
Na₂O	..	..	0·50	0·27	1·21
K₂O	..	..	5·81	8·17	7·46
H₂O+	..	..	5·56	4·00	4·53
H₂O-	..	..	1·37	0·40	0·43
TiO₂	..	..	0·70	0·13	abs.
P₂O₅	..	..	—	—	—
MnO	..	..	0·07	0·06	0·10
F₂	..	..	—	0·06	0·39
Less O=F₂	..	..	—	0·03	0·16
			100·50	99·62	100·07

The high potash of these analyses suggests the presence of mica which has been noted in the pinite or chloritic material of the spots in the Albury schists.

Both the New South Wales and Victorian rocks show a fine banding and a well-marked plication or false-cleavage. The pelitic layers usually contain an abundance of knots in a base consisting of elongated flakes of brown, green and white mica—no doubt the two-mica base described and analysed by Tattam (1929). The structure of this base is lepidoblastic. The intermediate sandy bands contain an abundance of quartz and show a tendency towards a granoblastic structure, although a parallelism of the mica flakes is apparent. Small elongated grains of quartz are also present in the pelitic layers and they sometimes become larger in the vicinity of the knots, where the texture of the pelite often becomes coarser. Iron ore and sphene are accessory, tourmaline is well developed in certain localities, and graphite is very abundant in some types.

Psammopelites and psammites show similar features. The schistosity is less well marked and there is a greater development of the granoblastic structure. The knots, so characteristic of the pelites, are not always developed in the interbedded psammite, but when present they consist almost exclusively of the green micaceous material and occur as large poikiloblastic porphyroblasts whose margins are interlocked with the xenoblastic quartz and micas surrounding them (Fig. 1, A and C).

These rocks appear to have suffered a fairly high-grade metamorphism which seems comparable in degree with the schists of the andalusite-zone at Cooma. In view of their advanced recrystallization, it seems probable that the micaceous and chloritic material
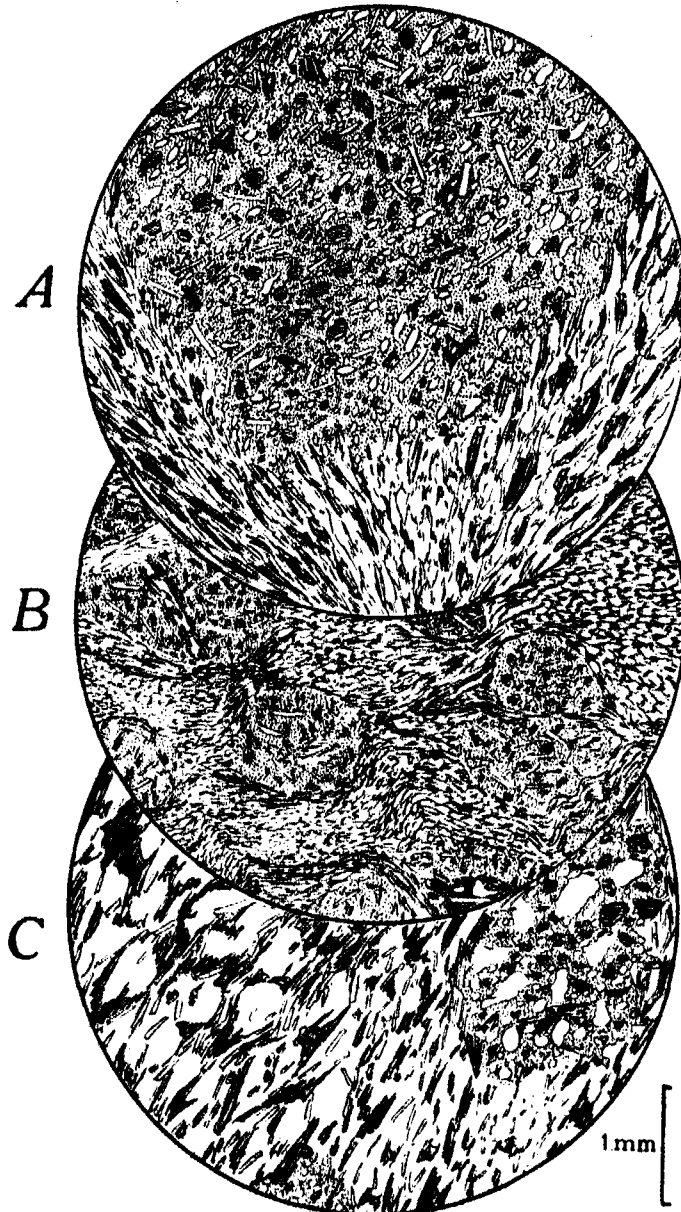
Fig. 1.—Knotted schists.

A. Psammopelite showing portion of a large knot. This consists of a mass of chlorite and sericite and contains numerous inclusions of biotite, muscovite and quartz. The base consists of elongated grains of quartz, biotite and muscovite which are bent around the knot. × 16.

B. Pelite showing numerous small knots, much altered and with a sieve-structure. The base has a marked schistosity with bending around the knots and consists of small elliptical grains of quartz and flakes of micas. × 16.

C. Psammite showing large altered knots with sieve-structure in a coarse base of quartz and mica having a marked schistosity. × 16.

of the knots represents a retrograde rather than an incipient change, in spite of the fact that the main body of the rock shows no sign of retrogressive metamorphism. There is little doubt, however, that the spots were originally cordierite and/or andalusite crystals, both minerals being far more susceptible to alteration than the micas of the base.

(c). Altered High-Grade Schists and Gneisses.

In the Cooma area, definite zones of permeation and injection could be mapped, but as the Albury area represents only part of a very much larger complex which has suffered the further complication of retrograde metamorphism, it is impossible to map either of these zones. Several types, however, may be recognized among the high-grade schists and gneisses and these will be described under the following headings:

(i). Greisenized schists and gneisses.

(ii). Granitized schists.

The latter show a somewhat different type of granitization from that observed at Cooma, and although permeation and injection have taken place, these schists cannot be classified as either permeation or injection gneisses as defined for the Cooma region. Gneisses here referred to are paragneisses or highly-altered sedimentary schists that have been soaked with igneous material. Orthogneisses and related contaminated types are described in the section dealing with the Ordovician intrusives (p. 97).

(i). *Greisenized Schists and Gneisses.*—These types occur along the Howlong Road to within half a mile of Bungowannah, and lie within the zone of sills, which have no doubt been partly responsible for the greisenization of the schists. There are slight indications that they may extend east of Albury, but as already noted (Joplin, 1944), the only good outcrops form the Eastern Hills at the back of East Albury.

These schists have suffered a high-grade metamorphism and often exhibit a coarse gneissic banding. Sillimanite is abundant, though it seems evident that some of it has developed after muscovite and andalusite and therefore followed the main period of high-grade metamorphism and of greisenization. Obviously the metamorphic history of this part of the country has been very complicated and a much larger area should be studied to arrive at reasonable conclusions regarding it.

The brown and green micas of the zone of knotted schists have now given place to deep red-brown biotite crowded with inclusions of zircon. When present, quartz forms large ellipsoidal grains, and biotite and muscovite occur in large parallel flakes up to 2 mm. in length. The muscovite is commonly poikiloblastic and often contains mats of sillimanite needles. In certain rocks the quartz is also crowded with sillimanite. A specimen from Eastern Hills contains large poikiloblastic porphyroblasts of pale pink andalusite. In hand-specimen it is not unlike the mottled gneiss from Cooma, and under the microscope shows some resemblances to that type, though it has suffered a severe retrograde metamorphism, some of the andalusite being altered to greenish mica and the original red biotite bleached and chloritized with the separation of iron ore and rutile. This rock occurs very close to a sill, and the retrograde changes can probably be attributed to this intrusion.

At Cooma the pink pleochroic andalusite appears to be of magmatic origin. Several of the high-grade rocks from Albury contain rose-pink andalusite surrounded either by mica or by sillimanite, and although no positive statement can be made, it seems likely that the andalusite originated in a permeation-zone like that of Cooma, and that the permeation gneisses have been subsequently altered either by the introduction of igneous material or by earth movement.

Orthoclase and a little altered cordierite have been detected in a few rocks that have not been completely greisenized just as in the permeation types of Cooma.

(ii.). *Granitized Schists.*—These rocks occur near Woomargama, on the steep hill on the Tumbarumba Road, 10 miles from Jingellic, near the Orphanage at Albury, and among the xenoliths in the two-mica gneiss at Albury. They appear to represent the soaking of high-grade psammites or psammopelites with magmatic material, and seem to correspond to Tattam's schistose hornfelses (Tattam, 1929, p. 17). In some cases large grains of orthoclase have developed in the schists and have either enveloped or pushed aside the original minerals of the rock. Subidioblasts of plagioclase, however, occur more

often as the indicator of this granitization process, which is comparable to the acidification processes observed in xenoliths (Nockolds, 1932). Quartz and muscovite also show evidence of having been derived from the igneous mass.

In the case of the permeation-gneisses of Cooma, the permeating magmatic material appeared to act as a vehicle bringing about changes within the rock, and there was rarely evidence of magmatic addition. In the Cooma injection-gneisses there was evidence of addition in the form of discrete *lits* or of veins. Granitization at Albury, however, is more of the nature of a mechanical permeation and is usually in the form of felspathization. The significance of this process will be referred to in connection with the origin of the Albury gneiss.

III. THE ORDOVICIAN INTRUSIVES.

1. THE SILLS AND SHEETS.

In describing the general geology of the Albury district (Joplin, 1944), it was pointed out that sills are very numerous among the Ordovician schists near Albury, and reference to the map (Plate xv) in the present paper will show that they have been mapped as a zone which is superimposed upon the higher grade metamorphic zones. In an earlier paper (Joplin, 1944, Fig. 1) a traverse along North Street shows sixteen sills of variable width in a distance of a quarter of a mile and a similar concentration of sills may be observed almost anywhere within the zone of sills. The size of the intrusions varies from the large Rocky Hill Sheet, which is about 600 feet in width, to smaller sheets of about 60 feet, down to sills of only a few inches. In these intrusions two main rock-types may be recognized. The Rocky Hill Sheet consists of an oligoclase granite, and the smaller sheets are usually composed of an aplite or microgranite in which oligoclase is a prominent constituent. The other type is a pegmatite grading on the one hand into a greisen and on the other into a schorl. One or other of these types usually constitutes a small single sill, and, as previously indicated (1944), the larger sills and sheets show sudden variations from fine aplite to coarse pegmatite, but there appears to be no regular arrangement with regard to the disposition of these types and they sometimes grade into one another. Very close examination of the sheets, however, suggests that the pegmatite is slightly later, the pegmatite veins possibly invading the sheets whilst they were still hot. Read (1931, p. 145) suggests a similar relation in the Loch Choire Complex.

In the general paper (1944) it was suggested that both the Rocky Hill granite and the Run Boundary granite occurred as Ordovician phacoliths since, where it is possible to discern their contacts, they appear to be concordant with the surrounding schists. Detailed petrographical work has confirmed this suggestion with regard to Rocky Hill, but, though sheet-like in habit, the Run Boundary granite appears to be more closely related to the younger granites, which are briefly described below (p. 119).

(a). Oligoclase Granites, Microgranites and Aplites.

This rock-type occurs in the sheets and larger sills, the Rocky Hill Sheet being the largest.

The Rocky Hill granite is invaded by pegmatite but the main mass is an oligoclase granite containing red garnet. The average grainsize is from 2–3 mm. and the fabric allotriomorphic granular, except for the garnet, which occurs in well-formed crystals which may be xenoblasts. The constituent minerals are quartz, oligoclase, orthoclase (sometimes microperthite and/or micropegmatite), biotite and muscovite with zircons as numerous inclusions in the biotite. Garnet forms small (0·5 mm. or less) idioblasts often associated with micas which occur in trails suggestive of resorbed sedimentary fragments, and partly sericitized grains of andalusite sometimes occur. Associated small areas of fine granular quartz also suggest a xenolithic origin for these minerals, although the occasional bending of micas and undulose extinction in quartz suggests that the fine patches may be due to granulation. The Rocky Hill granite shows variations from place to place and sometimes biotite is absent and the rock appears to grade into a pegmatite.

A sheet occurring on the track between Jindera Gap and Hamilton Trig. also contains red garnet, but in this case it occurs in large (2 mm.) irregular grains.

The sheet at the northern end of Eastern Hills is made up largely of oligoclase microgranite or aplite, but pegmatite-injection appears to have followed closely. This has a grainsize of about 0·75 mm. and is hypidiomorphic granular. It contains quartz and small grains of microcline and the oligoclase is idiomorphic against these. Sericitized grains of andalusite associated with trails of muscovite suggest sedimentary rafts. A somewhat similar type occurs in the large sill which has been quarried at the western end of North Street, but here the pegmatitic phase is more prominent. Obviously, these rocks are slightly contaminated, though far less so than the gneisses described below, and it is likely that the original magma contained only the ingredients of quartz, oligoclase and potash felspar.

These rocks compare in composition with the quartz-felspar injection type described and analysed by Tattam (1929, pp. 25 and 38), who refers to the occurrence of garnets in an acid leucocratic type at Kergunyah Gap (p. 24), Tawonga (p. 25), and in the Mitta Mitta Region (p. 27). A muscovite granite from Omeo is evidently of the same magma-type and is compared in Table 6. Furthermore, these rocks bear a close chemical resemblance to the albite-muscovite gneiss at Cooma (Joplin, 1942, p. 189), which was believed to represent an altered phase of the Cooma gneiss, but in view of the composition of the Albury sheets, is now considered to be a separate marginal injection of this magma-type. Reference to Table 6 will show that alumina is a little high for rocks of this silica percentage. Furthermore, alkalies are high, and although potash is

TABLE 6.

			I.	II.	III.	IV.	V.
SiO_2	..	..	72·71	73·99	72·85	76·10	73·66
Al_2O_3	..	..	17·07	16·08	15·83	15·05	17·89
Fe_2O_3	..	..	0·05 }	0·65	0·25 }	tr.	tr.
FeO	..	..	0·90		0·14		
MgO	..	..	0·29	0·31	0·17	0·11	0·09
CaO	..	..	0·14	0·09	0·51	0·23	0·27
Na_2O	..	..	3·09	3·67	3·31	2·90	2·36
K_2O	..	..	4·34	4·04	5·68	3·27	5·12
H_2O+	..	..	0·43	0·45	0·76	0·98	0·58
H_2O-	..	..	0·08	0·06	0·23	0·18	0·07
TiO_2	..	..	abs.	abs.	tr.	—	n.d.
P_2O_5	..	..	0·41	0·43	0·21	—	0·02
MnO	..	..	0·35	tr.	tr.	—	tr.
BaO	..	..	—	—	0·06	—	—
			99·86	99·77	100·00	99·72	100·06
Sp. Gr.	..	..	2·66	2·66	—	2·673	2·67

I. Garnet-bearing Oligoclase Granite. Rocky Hill, Por. 126, Par. of Mungabarina. Anal. G. A. Joplin.

II. Oligoclase-microcline Granite. Quarry near Saleyards, Eastern Hills, Por. 107, Par. of Albury. Anal. G. A. Joplin.

III. Quartz-felspar Injection Type. Tawonga. Anal. C. M. Tattam. *Geol. Surv. Vict.*, Bull. 52, 1929: 38.

IV. Muscovite Granite. Near Hinnomunjie Morass, Omeo. Anal. A. W. Howitt. *Trans. and Proc. Roy. Soc. Vict.*, 24, 1887.

V. Albite-muscovite Gneiss. Dry Plain Road, Por. 161, Par. of Binjura. Anal. G. A. Joplin. PROC. LINN. SOC. N.S.W., 67, 1942: 188.

always a little in excess of soda, they are not strikingly different, as is the case in the pegmatites (Table 7). Comparison of these two tables will show that although the silica percentage is approximately similar in both rock-types they differ with regard to alumina, magnesia and alkalies, especially with respect to potash and soda. Although closely associated in the sills and sheets the oligoclase granites, therefore, appear to represent a distinctly different magma from that which gave rise to the pegmatites, although they may be related by differentiation.

The chemical uniformity of the oligoclase granites almost precludes the possibility of much contamination, and the analyses in Table 6 probably represent a true magma-

type, although it is shown below (Table 12) that with extensive contamination a certain degree of stability may be reached and a fairly uniform rock-type formed.

(b). Pegmatites, Greisens and Schorls.

The field relation of the pegmatites and oligoclase granites and aplites has already been discussed. In hand-specimen the former are either coarse and massive or may show a graphic structure which may be very coarse or extremely fine. In the coarse graphic types grains of microcline may measure over 2 inches, but in the more common finely graphic types they average about 2 mm. with the intergrown quartz units measuring about 0·5 mm. or less. Sometimes the quartz shows slight granulation or undulose extinction indicating some post-consolidation movement, but this is not a notable feature as is the case in the Cooma pegmatites. Sometimes tourmaline forms a fine graphic intergrowth with the quartz units, which are themselves intergrown with the microcline. In some rocks the microcline is partly albitized and is thus a microcline-microperthite. Reference to Table 7, Anal. IV, will show that the soda is a good deal higher and the potash correspondingly lower in the albitized type. Oligoclase and muscovite are usually present in varying amount and biotite is occasionally present.

TABLE 7.

				I.	II.	III.	IV.
SiO$_2$	..	..	..	74·26	74·71	70·91	71·94
Al$_2$O$_3$	..	..	..	14·87	15·51	15·32	15·71
Fe$_2$O$_3$ } Fe0 }	..	..	..	0·20	tr.	tr.	0·35
MgO	..	..	..	0·03	abs.	0·07	tr.
CaO	..	..	..	0·25	0·34	0·58	0·34
Na$_2$O	..	..	..	1·81	1·59	2·31	4·41
K$_2$O	..	..	..	8·39	8·11	10·07	7·58
H$_2$O +	..	..	..	0·37	0·10	0·36	0·20
H$_2$O -	..	..	..	0·07	0·03	0·15	0·01
TiO$_2$	..	..	..	abs.	n.d.	—	abs.
P$_2$O$_5$	..	..	..	abs.	0·10	—	0·06
MnO	..	..	..	abs.	abs.	—	tr.
				100·25	100·49	99·77	100·60

I. Graphic Pegmatite. Albury Common, Black Springs Creek, Pors. 43/45, Par. of Albury. Anal. G. A. Joplin.

II. Graphic Pegmatite. Soho Street, Cooma. Anal. G. A. Joplin. PROC. LINN. Soc. N.S.W., 67, 1942 : 188.

III. Graphic Granite. Wilson's Creek, Omeo. Anal. A. W. Howitt. Trans. and Proc. Roy. Soc. Vict., 24, 1887.

IV. Albitized Graphic Pegmatite. Quarry near Saleyards. Por. 107, Par. of Albury. Anal. G. A. Joplin.

With increase in muscovite and an accompanying decrease in felspar the rocks grade into greisens—books of white mica often measuring an inch or more across. In some types the muscovite is plumose in its development and radiating masses may measure up to 3 inches. With increase in tourmaline the pegmatites grade through tourmaline pegmatites into schorls. In thin section the tourmaline is blue or brown and often zoned. In the coarser types of schorl or pegmatite the tourmaline crystals measure over 2 inches in length. Small veins of almost pure tourmaline frequently cut the two-mica gneiss and these may be seen very well on the Howlong Road between the west end of Smollett Street and the West Albury Post Office.

2. THE CONTAMINATED GNEISSES.

Reference to the map (Plate xv) will show that gneisses occur within the town of Albury beneath Monument Hill, on the shore of the northern arm of the Hume Reservoir, near Woomargama, and north of Jingellic about 10 miles along the Tumbarumba Road.

All these gneisses are contaminated with sedimentary material and among them two types are recognized—one characteristically containing cordierite, the other a more acid type particularly rich in mica. The latter bears a close resemblance to the Cooma gneiss.

(a). Cordierite-bearing Gneisses.

This type is developed along the northern and western shore of the Bowna Arm of the Hume Reservoir and large remnants of it occur in a younger granite which has been quarried for the construction of the dam wall. Fresh material from this quarry has been briefly described in an earlier paper (Joplin, 1944), where it was pointed out that it bore such a close resemblance to the Bethanga gneiss of Victoria, described by Tattam, that it seemed desirable to use the same name.

Further, in this earlier paper it was suggested that the gneiss developed on the western shore of the reservoir north of the quarry was possibly another type. Though deeply weathered, it appeared to be non-porphyritic, to contain no garnets and often to show *lit-par-lit* injection. In view of this uncertainty it was tentatively named the Bowna gneiss. Since examining a still more northerly mass, however, it seems fairly evident that it is a local phase of the cordierite-bearing gneiss, though the weathering prevents the recognition of some of the characteristic minerals.

Both field and microscopic studies point to the contamination of the cordierite-bearing gneiss, and before proceeding to a description of the gneiss, it is desirable first to examine the xenoliths which are very numerous and are no doubt responsible for the contamination.

i. The Xenoliths.

Xenoliths of all sizes and degrees of resorption occur within the cordierite-bearing gneiss. They are best studied in the quarry, Por. 65, Parish of Thurgona, where two main types may be recognized—a basic granulite and an aluminous pelite. The former usually forms the larger inclusions and may measure up to 2 feet across. The smaller pelitic xenoliths are by far the numerous and the most modified. They show considerable resorption and variation in size and are often represented only by tiny wisps, a single microsection often containing several in different stages of resorption. The pelites also show differences of composition, there being present silica-rich and silica-poor types.

(a). *Granulites.*—The granulites present evidence of strong thermal metamorphism, but there is little evidence of assimilation—a fact noted with regard to the basic granulites at Cooma (Joplin, 1942), where reference was made to similar observations by Read (1927). Three types of granulite have been recognized and these are frequently interbedded. A pyroxene-bearing type possibly represents a basic igneous rock—a basalt or dolerite (see Table 4, Anal. I); a garnet-bearing type may represent an admixture of sedimentary and basic igneous material and is possibly tuffaceous; and a plagioclase-biotite assemblage appears to be a related type still richer in the sedimentary material (see Fig. 2).

The pyroxene granulites are dense, granular rocks varying from dark purplish-grey to a greenish colour according to the presence or absence of biotite. Under the microscope these rocks are often seen to be blastoporphyritic in plagioclase, large (3 mm.), recrystallized grains of labradorite ($Ab_{35}An_{65}$) occurring in a granoblastic groundmass of labradorite, diopside, biotite, magnetite, apatite and quartz (Fig. 2, A). The original felspar phenocrysts show nibbled margins, complicated interpenetration twinning and irregular inclusions of quartz. Sometimes the felspar shows alteration to white mica. Reference to Table 4 will show that this rock compares with rocks of the Porphyritic Central Magma Type (Bailey and Thomas, 1924) which is characterized by the development of plagioclase phenocrysts.

The plagioclase of the groundmass is not well twinned and often occurs in irregular grains (0·15–0·6 mm.) intergrown with diopside, biotite and quartz. Quartz grains are sporadic in their distribution and those occurring as inclusions in the larger felspars are comparable in size with those of the groundmass.

A type without biotite is much richer in quartz, suggesting an admixture of psammitic material. Diopside is usually fresh, but in certain banded types, alteration to an amphibole occurs and seems to mark the first stage in the disintegration of the xenolith. In certain types the quartz and felspar show slight elongation and the schistosity is further emphasized by the amphibolization of the pyroxene, some of which may have

developed prior to assimilation. In some types sphene is abundant, especially in the case of biotite-poor varieties, thus suggesting the entrance of titania into the biotite-molecule.

The most common type of granulite is a garnet-plagioclase-biotite-quartz assemblage (Fig. 2, B), but a good deal of variation is shown in the relative abundance of these four
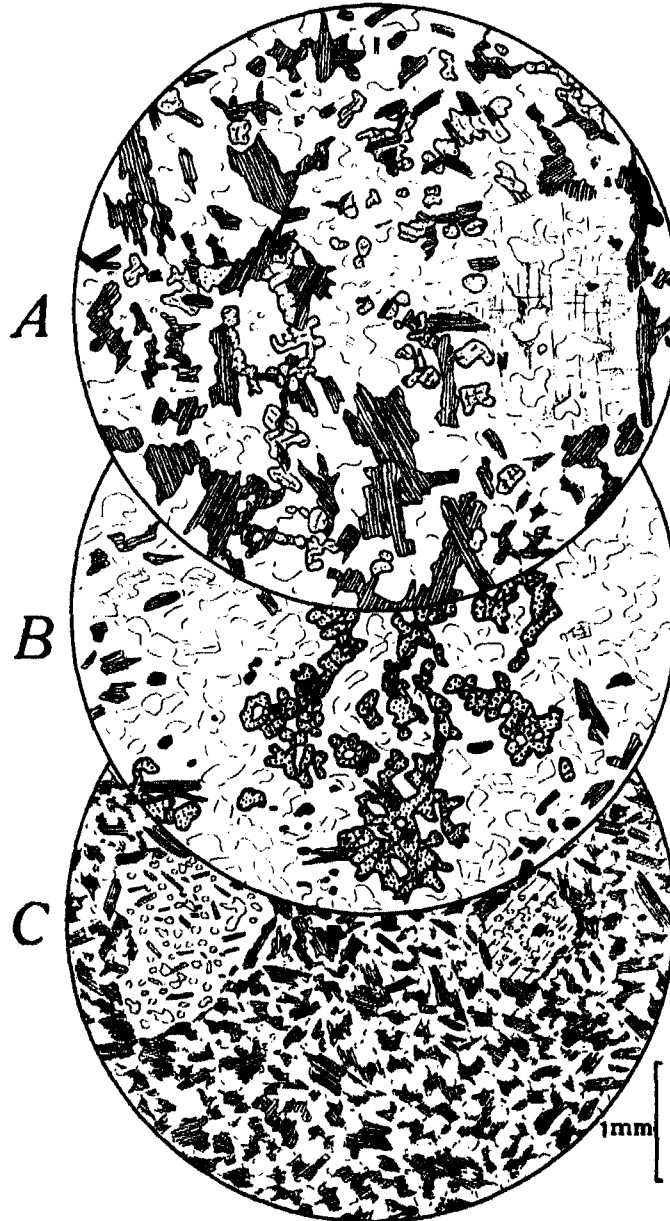
Fig. 2.—Granulite xenoliths.

A. Granulite showing blastoporphyritic structure; a large crystal of labradorite, on the right, is surrounded by a granoblastic groundmass of diopside, biotite, plagioclase and quartz. × 16.

B. Granulite consisting of a granoblastic mass of garnet, plagioclase, biotite, quartz and magnetite. × 16.

C. Granulite showing large porphyroblasts of plagioclase with a sieve-structure in a granoblastic mass of biotite, plagioclase and quartz. × 16.

constituents. Magnetite is usually a minor accessory, but may be fairly abundant in some types. Red garnet forms irregular poikiloblasts and sometimes shows alteration into chlorite. This alteration is particularly common in banded types that also show alteration of pyroxene to amphibole and may thus evidence either dynamic metamorphism or reaction.

Occasionally a granulite, consisting of red-brown biotite, basic plagioclase and quartz, occurs interbedded with the garnet-bearing or pyroxene-bearing varieties. These rocks are usually finer in grainsize, but may contain large porphyroblasts of plagioclase exhibiting a sieve-structure (Fig. 2, C).

(b). *Pelites.*—Aluminous pelites are by far the most numerous and the most modified of the xenoliths in the cordierite-bearing gneiss, and, as noted above, both silica-poor and silica-rich types occur.

All these xenoliths are strongly metamorphosed and usually show evidence of reaction with the gneissic magma. Although it is impossible completely to separate the two processes, and there has undoubtedly been an overlap in the time that each occurred, an attempt will be made to describe first the changes brought about solely by thermal or pyrometamorphism, and then those due to reaction.

The most common type of xenolith is a cordierite-sillimanite-spinel assemblage in which red-brown biotite is a prominent constituent. This rock may be banded, some seams richer in sillimanite and others in cordierite, and this difference can no doubt be correlated with seams of slightly different composition in the original sediment (Fig. 3, A, B). The sillimanite occurs as matted skeins of elongated fibres or as stout rods with a diagonal cleavage in cross-section. Cordierite forms large irregular grains enclosing the other minerals (Fig. 3, B) or as groups of small irregular grains. Zircons, surrounded by pleochroic halos, are common inclusions. The cordierite is very susceptible to alteration, and although the alteration products have not all been satisfactorily determined, sericite, chlorite and isotropic pinite have been recognized. Spinel forms
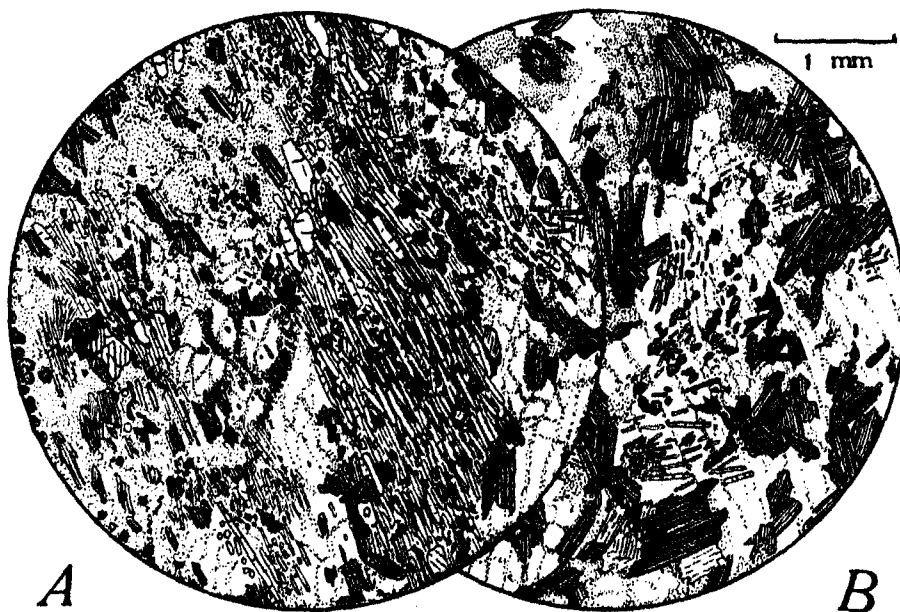
Fig. 3.

A. Banded hornfels xenolith showing seams of sillimanite-spinel-biotite-magnetite and cordierite-sillimanite-spinel-biotite-magnetite assemblages. Note partial alteration of cordierite. × 16.

B. Xenolith showing large crystals of cordierite enclosing spinel, sillimanite, biotite and magnetite. Smaller grains of cordierite, partly altered, also occur. At the top of the figure the contaminated gneiss consisting of quartz, biotite and altered cordierite, is adjacent to the xenolith which is fringed by larger flakes of biotite. × 16.

clusters of small octahedral crystals or minute irregular grains which vary in colour from light to dark green or to purplish-brown. They are usually associated with aggregates of magnetite granules and sometimes mantle the iron ore. Biotite, evidently rich in the haughtonite-molecule, occurs in small irregular flakes within the cordierite or is intergrown with the sillimanite. Sometimes it forms large flakes surrounding the xenolith and appears to have developed as a result of reaction with the magma (Fig. 3, B). Inclusions of zircon are abundant in the biotite.

Silica-rich assemblages are interbedded with silica-poor seams and two types containing red garnet have arisen as the result of the pyrometamorphism of the silica-rich aluminous pelites. These are garnet-sillimanite-cordierite and garnet-cordierite assemblages. Red-brown biotite is characteristic of both types and the cordierite shows features similar to those described above. The garnet forms large irregular grains which may measure up to 10 mm. It is usually surrounded by a narrow margin of chloritic material and is frequently in direct contact with quartz grains (Fig. 4, A). Occasionally the garnet is clouded with filaments of sillimanite, a feature observed by Tattam (1929, p. 28) in the Bethanga gneiss of Victoria. Miss Helen McRoberts, B.Sc., has kindly determined the refractive index of this garnet as 1·80, and the chemical composition is as follows:

				Metal Atoms on basis of 12 O.		Ideal Composition.		
SiO₂	..	..	37·30	2·94	0·06 ⎫ 3·00	3		Sp. Gr. = 4·085
Al₂O₃	..	..	22·55	2·09	⎰			n. = 1·80
					2·03 ⎭ 2·03	2		
TiO₂	..	..	tr.	—				
Fe₂O₃	..	..	3·07	0·18 ⎫			Almandine .. 67·73	
FeO	..	..	27·78	1·83 ⎪			Pyrope .. 16·48	
							Spessartine .. 6·41	
MgO	..	..	4·91	0·58 ⎬ 2·87	3		Grossular .. 3·15	
							Sillimanite .. 5·75	
MnO	..	..	2·79	0·18 ⎪			99·52	
CaO	..	..	1·15	0·10 ⎭				
			99·55					

From the above calculation it would seem that the whole of the ferric iron enters the group of divalent elements, and Alderman (1935) has noted that this substitution is common in almandine-rich garnets. The calculation further shows that the analysis is a little low in the divalent elements, and this would in part account for the presence of the large proportion of normative sillimanite, though it was noted that this mineral was often present as minute inclusions in the garnet, and it is possible that the analysed sample had not been completely freed from them. Reference to Alderman's diagram (1936, Fig. 3) will show that this garnet, rich in the almandine and spessartine molecules, falls within the composition field of the garnets characteristic of sedimentary schists.

As mentioned above, it is difficult to dissociate completely the effects produced by thermal metamorphism from those due to reaction with the magma, and matters are further complicated by changes that may have been superimposed by the later invasion of the younger (Hawkesview) granite.

An early stage in the assimilation of the garnetiferous xenoliths is marked by the development of green mica along cracks in the garnet, and finally, by the separation of minute magnetite granules (Fig. 4, B). Nevertheless, garnet appears fairly stable and other minerals associated with it in the hornfels-stage disappear first, isolating the large irregular garnets which thus appear to be the products of crystallization from a contaminated magma. In handspecimen the cordierite-bearing gneiss exhibits patches of red garnet up to half an inch in diameter, and their origin is attributed to this cause. The red-brown biotite of the original hornfels becomes bleached or chloritized during assimilation and there is a concomitant separation of rutile needles in the form

I

of a sagenite-web. The cordierite is completely broken down into chlorite, sericite and pinite (Fig. 4, B).

The silica-poor xenoliths show a more marked reaction with the magma. Again, the cordierite becomes changed into chlorite, sericite and pinite, and this change appears to have taken place long before the sericitization of the sillimanite, unaltered sillimanite

1 mm

Fig. 4.

A. Banded xenolith showing seams of silica-poor and silica-free hornfels. A large irregular grain of garnet, bordered by chlorite and intimately associated with quartz, occurs in a cordierite-biotite assemblage and this adjoins a type consisting of spinel, sillimanite and altered cordierite. × 16.

B. Xenolith of garnet-cordierite-biotite hornfels showing reaction with enclosing magma. The small mass of garnet, just above the centre of the figure, shows alteration into chlorite and magnetite granules, cordierite is sericitized and chloritized and biotite is chloritized and bleached. In the lower part of the figure the gneiss, consisting of orthoclase and quartz, shows chloritization and sericitization of the felspar. × 16.

occurring with spinel, biotite and magnetite in a base of sericite and chlorite (Fig. 5, B). Large flakes of muscovite may develop within the xenolith and these seem to be a product of interaction between xenolith and magma rather than one of magmatic crystallization (Fig. 5, A). Schistosity and plications are often preserved within the xenolith even after much reaction has taken place. Spinel is very stable and often occurs as small granules in wisps of chlorite and sericite that mark the position of an almost completely resorbed fragment. The final product of reaction is a criss-cross mass of mica in which muscovite is the most important constituent.

Spinel-bearing xenoliths are not uncommon in basic igneous rocks (Read, 1932), but it is very unusual for them to occur in a rock so acid as the cordierite-bearing gneiss (Table 8, Anal. I). Moreover, their development is even more puzzling in that there is no evidence of silica-poor types among the original sediments, unless such occur as restricted bands among the normal pelites. Tattam (1929) refers to the occurrence of spinel in the "clots" of the Bethanga gneiss of Victoria, but makes no attempt to explain the anomaly. This matter is discussed further, below, where some attempt is made to account for the genesis of this assemblage.

ii. *The Gneisses.*

In handspecimen the cordierite-bearing gneiss is a porphyritic rock with the phenocrysts varying both in size and concentration. Large clusters of red garnet up
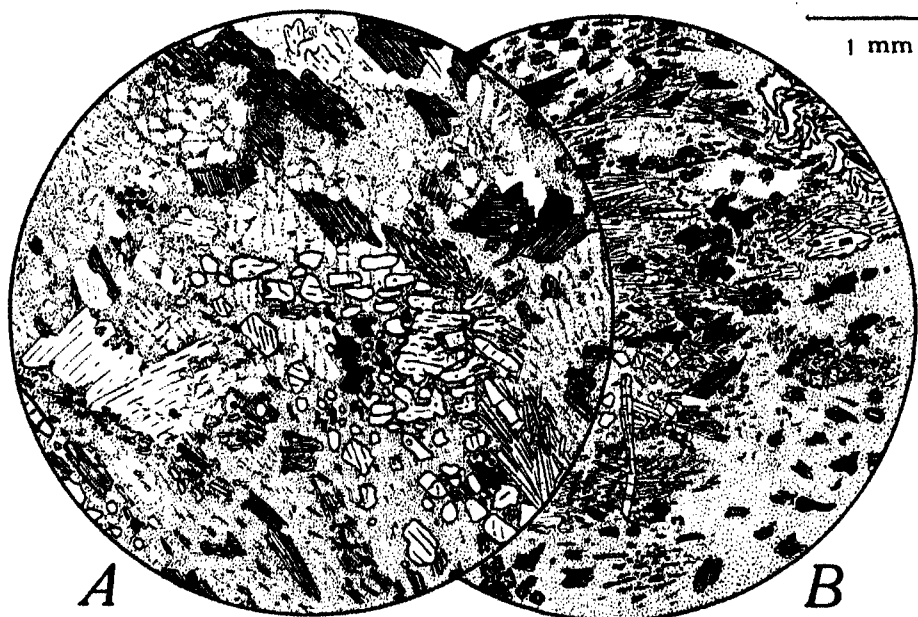
1 mm

Fig. 5.

A. Cordierite-sillimanite-biotite-spinal xenolith showing alteration of cordierite and development of large flakes of muscovite. Spinel is not well represented in this field, but is more abundant elsewhere in the slide. × 16.

B. Later stage in the resorption of the same xenolith. Plication of original schist is visible in NE. quadrant where sillimanite occurs in the fold axes. Sillimanite, spinel, magnetite and biotite occur in a mass of chlorite and sericite which represents altered cordierite. The remains of a little fresh cordierite are seen near the top of the figure and pleochroic halos about zircon inclusions are visible. × 16.

to half an inch across are common and the rock is crowded with xenoliths of all sizes and in all stages of disintegration. The lighter part of the gneiss has a slightly greasy greenish appearance which is no doubt due to the presence of cordierite. This mineral may be in part xenocrystal, but the greater part of it appears to be pyrogenic and to have crystallized from the contaminated magma. Although the gneiss has a fairly uniform mineral constitution, it shows a great deal of variation both in grainsize and in the relative proportions of the minerals present. This is to be expected in a highly-contaminated rock in which xenoliths of different composition are present in various stages of assimilation. Nevertheless, a type showing some degree of uniformity is regarded as a close approach to the end-product of assimilation, and this type may be called a cordierite-bearing gneiss.

In the immediate vicinity of the pelitic xenoliths heavy chloritization and greisenization of the orthoclase, and sometimes of the less abundant plagioclase, is apparent. The biotite is chloritized and bleached with separation of rutile in the form of a sagenite-web (Fig. 6, A). The altered cordierite associated with this contaminated phase is probably xenocrystal and represents fragments wedged off from the xenolith.

Another highly-contaminated type, usually in juxtaposition to a xenolith of aluminous pelite, consists largely of fairly fresh cordierite, large flakes of red-brown biotite, red garnet (sometimes containing mats of sillimanite needles) quartz, usually orthoclase and a certain amount of chlorite.

The two types referred to above are obviously highly contaminated and bear no resemblance to an igneous rock, but the cordierite-bearing gneiss described below is essentially igneous, and although not a true representative of the original magma, it is the closest approximation that could be obtained, and the analysis given in Table 8 represents a rock from which all macroscopic xenoliths and garnets have been removed.

It is thus freed from material causing mechanical contamination and the chemical composition is believed to reflect the chemical contamination.

Under the microscope the rock is porphyritic and the average grainsize of the groundmass is about 2 mm. The phenocrysts consist of orthoclase and the groundmass is made up of quartz, orthoclase, andesine, cordierite, biotite, muscovite, chlorite, sericite, magnetite, zircon and rutile. Myrmekite is sometimes present, and the presence of sillimanite rods associated with sericite, chlorite and cordierite indicates an unstable assemblage in which reaction has not reached completion.
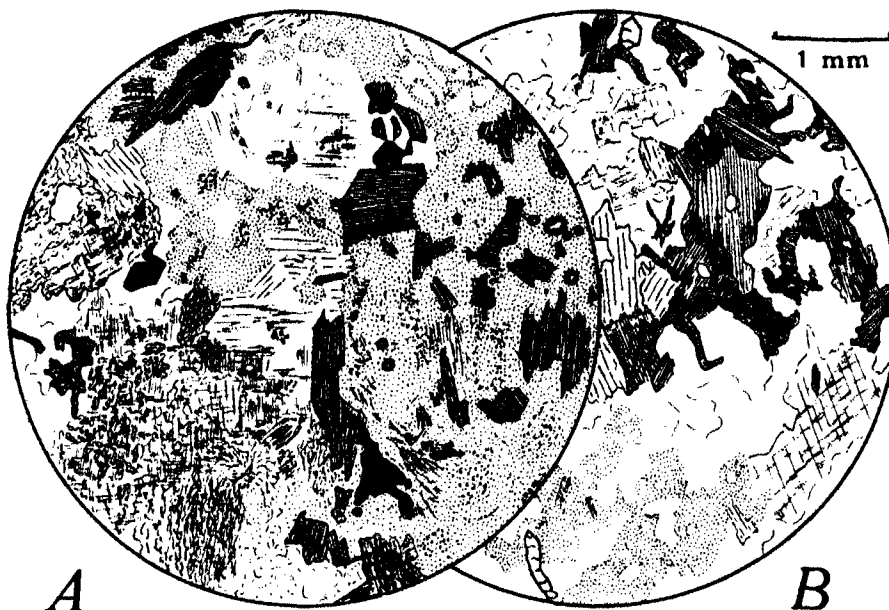

Fig. 6.

A. A highly-contaminated gneiss at margin of xenolith. A small cluster of spinel granules, near the top of the figure, is embedded in altered cordierite, marking the remains of a xenolith which extends down the right side of the figure. It consists mainly of altered cordierite, with pleochroic halos, and biotite. A little fresh cordierite is present in the NE. quadrant. At the margin of the xenolith, orthoclase is both chloritized and sericitized, plagioclase is unaffected and biotite is bleached with a separation of rutile needles. × 16.

B. Contaminated gneiss consisting of quartz, plagioclase, orthoclase, muscovite, biotite (partly altered), subidiomorphic pyrogenic cordierite (completely altered), apatite and zircon. × 16.

Part of the crystallization of the orthoclase phenocrysts appears to have been contemporaneous with that of the groundmass minerals, for there is an interlocking of the mineral grains about the margins of the phenocrysts. Some phenocrysts, containing numerous rounded grains of quartz and small flakes of red-brown biotite, suggest that the felspar has wedged apart and enveloped a granulite xenolith. Sometimes a fan-shaped mass (3 mm. in length) of sillimanite represents the envelopment of an aluminous pelite xenolith. Orthoclase also occurs as irregular grains in the groundmass where it is usually interlocked with quartz, andesine and cordierite. Marginal incursions of myrmekite are common and very small areas of graphically intergrown quartz sometimes occur. The orthoclase often shows alteration into sericite and kaolin and is occasionally almost completely pseudomorphed by these minerals.

Quartz is abundant and forms large irregular grains often acting as wedges in the mechanical disintegration of the xenoliths (Nockolds, 1933). Small quartz grains occurring as inclusions suggest a sedimentary origin.

Andesine ($Ab_{65}An_{35}$) usually forms irregular grains intergrown with the other minerals of the groundmass, but may form large grains which help further in the

process of mechanical disintegration of the xenolith. Periclase twinning is sometimes present in addition to the albite-type and sericitization of the plagioclase is fairly common.

Cordierite, fresh, partly altered, or completely pseudomorphed, is a constant constituent of the cordierite-bearing gneiss, and though in some instances it appears to be xenocrystal, it seems more often to have crystallized from a highly-contaminated magma. The cordierite, or its pseudomorphs, is subidiomorphic against quartz and felspar, thus suggesting a pyrogenic origin (Fig. 6, B). Alteration to a chloritic material, possibly pinite, and to sericite is common, and when both types of alteration are present, sericitization follows pinitization. Inclusions of zircon are frequent and these show pleochroic halos both in the fresh cordierite and in its pseudomorphs. The outcrop of gneiss on the northern end of the Bowna Arm of the reservoir contains abundant cordierite showing alteration into bright orange, isotropic pinite, but owing to the weathering of most of these rocks, their petrography has not been studied in detail. It seems certain, however, that they represent a northern continuation of the gneiss examined at the quarry and they can certainly be grouped with the cordierite-bearing gneisses, though their cordierite is usually xenocrystal.

Biotite occurs in red-brown flakes as well as in masses of chloritized and bleached flakes containing a sagenite-web of rutile needles and sometimes elongated granules of sphene. Lenses of chlorite are very common and there is some suggestion that the groups of bleached flakes represent an earlier unstable crystallization of magmatic biotite not completely in equilibrium with a magma which is becoming more and more contaminated. Red-brown biotite, probably rich in the haughtonite-molecule, is probably a stable crystallization from the contaminated magma. This point, however, is still open to doubt as the red biotite occasionally appears to be breaking down in the same way. Nevertheless, this alteration may belong to a much later period when the cordierite-bearing gneiss was engulfed by the Hawksview granite. Zircon inclusions with their characteristic pleochroic halos are always present.

Muscovite occurs as independent flakes up to about 1·5 mm., and is sometimes in parallel intergrowth with biotite. It also occurs in radiating tufts in masses of sericite which is the alteration product of felspar and cordierite.

Apatite is sporadic in its occurrence and may be quite abundant, forming crystals up to 0·5 mm. across.

TABLE 8.

				I.	II.	III.	IV.
SiO$_2$	..	..	..	66·94	66·68	67·41	66·80
Al$_2$O$_3$	..	..	..	16·65	16·50	15·76	15·80
Fe$_2$O$_3$	..	..	..	0·40	2·41	1·93	1·62
FeO	..	..	..	4·77	1·93	1·96	3·63
MgO	..	..	..	2·19	1·44	1·43	2·25
CaO	..	..	..	0·94	3·51	3·54	0·47
Na$_2$O	..	..	..	2·11	4·08	3·45	1·00
K$_2$O	..	..	..	3·56	2·56	3·76	5·02
H$_2$O +	..	..	..	2·13	—	—	2·10
H$_2$O −	..	..	..	0·12	—	—	0·34
TiO$_2$	..	..	..	0·60	0·58	0·51	0·69
P$_2$O$_5$	..	..	..	0·01	0·15	0·19	0·66
MnO	..	..	..	0·06	0·06	0·06	0·08
Etc.	..	..	..	—	—	—	0·14
				100·48	100·00	100·00	100·60

I. Cordierite-bearing Gneiss. Weir Quarry, Por. 65, Par. of Thurgona. Anal. G. A. Joplin.

II. Average Dacite (90 analyses). R. A. Daly, Igneous Rocks and the Depths of the Earth, p. 457.

III. Average Quartz Monzonite (20 analyses). Ibid.

IV. Felspathic Pinite-gneiss (contaminated Granitic Gneiss). Essay. Anal. C. M. Tattam. Geol. Surv. Vict., Bull. 52, 1929 : 38.

The analysis of the cordierite-bearing gneiss shows it to be an intermediate rock, but the excess of magnesia over lime and of potash over soda indicates that it is not a normal type and has arisen as the result of magmatic contamination, magnesia and potash having been derived from the xenolithic material.

In Table 8 the analysis of the cordierite-bearing gneiss is compared with the average analyses of two common normal igneous rocks, both members of the grano-diorite clan, and having a silica percentage similar to that of the gneiss. In Table 9 the norms of these three analyses are compared, and the greater amount of corundum and of hypersthene in the gneiss bears striking testimony to the fact that cordierite is present in the mode. In the normal, uncontaminated rocks the higher lime and soda are further responsible for the lower corundum as these combine with the alumina to give the greater amounts of anorthite and albite, respectively.

TABLE 9.

				1.	II.	III.
Quartz	..	..	..	32·22	23·22	23·22
Orthoclase	..	..	..	21·13	16·12	22·24
Albite	..	..	..	17·82	34·06	28·82
Anorthite	..	..	..	4·73	16·68	16·68
Corundum	..	..	..	7·65	0·82	—
Hypersthene	..	..	..	12·89	5·81	4·95
Magnetite	..	..	..	0·70	3·48	2·78
Ilmenite	..	..	..	1·22	1·22	0·91
Apatite	..	..	..	—	0·34	0·34

iii. *The Contamination Process.*

Obviously the magma has been contaminated by the addition of magnesia, alumina and potash. The addition of magnesia finds mineralogical expression in the chloritization of felspars and of biotite and in the development of pyrogenic cordierite. According to Tilley (1940), the idiomorphic outline of the cordierite in the pegmatites from the moraines of Cape Denison, Antarctica, indicates that it has crystallized from a contaminated magma, and is not xenocrystal material; and a similar origin is suggested by the subidiomorphic development of the cordierite in the cordierite-bearing gneiss. The cordierite of the cordierite-aplite and pegmatite of Broken Hill (Browne, 1922) is also believed to be pyrogenic. The altered cordierite in the gneiss on the northern shore of the reservoir in the Parish of Bowna is, however, probably xenocrystal and the contamination process purely a mechanical one.

In the cordierite-bearing gneiss of the quarry the orthoclase forms phenocrysts and these often show chloritization as a result of reaction with the xenoliths, so it seems likely that this felspar had started to crystallize before the liquid fraction had been much affected by contamination.

It is reasonable to assume that both granulite and pelite xenoliths have played their part in the contamination process. Although the latter xenoliths are smaller and appear to be more numerous, this might be explained by the fact that the granulites were more readily assimilated and the larger, comparatively unaltered masses now present are those that were caught up by the magma during the late stages of its crystallization after reaction had ceased. The pelites on the other hand represent the small fragments that the magma was unable to digest after a good deal of reaction and mechanical disintegration had taken place.

Bowen (1922) and Nockolds (1933) have shown that if a xenolith contains minerals that represent phases lower in the reaction series than those with which the magma is in equilibrium, then they tend to become part of the magma by precipitating phases with which it is saturated. This process also assists in the mechanical disintegration of the xenolith.

It has been shown that the granulites consist usually of labradorite, diopside, biotite, quartz, magnetite and apatite. Biotite and quartz would probably be lower in the reaction series than the minerals being precipitated by the magma, whilst the plagioclase and diopside would readily react with it to give a more acid plagioclase and a greater

quantity of biotite, thus enriching the magma in lime and magnesia. These reaction processes would have been accelerated by the disintegration of the xenolith owing to the melting out of the low-phase constituents, quartz and biotite; the effect is thus twofold.

In the case of the pelitic xenoliths, the process would have been again both mechanical and chemical, but as the composition of these rocks is so much further removed from that of an igneous magma, it is not surprising to find them a little less digestible. Thus the magma was not always able to deal with the large quantities of alumina introduced, and though much sericitization of sillimanite has taken place, some still remains unaltered in the incompletely resorbed xenoliths.

Table 10 shows the analysis of a spinel-bearing xenolith where it is compared with xenoliths and contact rocks from other parts of the Victorian Complex and with the average analysis of eleven normal pelites—the sedimentary type from which it was

TABLE 10.

			I.	II.	III.	IV.	V.
SiO$_2$	..	..	52·36	54·22	55·94	58·87	56·07
Al$_2$O$_3$	..	..	25·81	21·01	23·39	16·95	23·65
Fe$_2$O$_3$	..	..	1·78	1·79	0·45	8·62 ⎫	6·79
FeO	..	..	7·03	5·61	4·69	3·93 ⎭	
MgO	..	..	3·41	2·43	3·58	2·32	2·83
CaO	..	..	1·49	0·49	0·81	0·07	0·39
Na$_2$O	..	..	1·15	1·75	1·45	1·48	0·68
K$_2$O	..	..	4·11	7·41	6·98	5·98	5·90
H$_2$O+	..	..	0·90	2·46	3·17	— ⎫	2·70
H$_2$O−	..	..	0·39	0·36	0·43	—·· ⎭	
TiO$_2$	..	..	1·38	1·78	—	—	0·72
P$_2$O$_5$	..	..	tr.	0·31	0·10	· ·	0·13
MnO	..	..	n.d.	0·14	··	—	0·05
			99·90	99·76	100·99	99·12	100·00

I. Sillimanite-cordierite-spinel Xenolith in Bethanga Gneiss. Hume Reservoir Quarry, Por. 65, Par. of Thurgona. Anal. G. A. Joplin.

II. Micaceous Xenolith in Granite. Mt. Wagra. Anal. C. M. Tattam. *Geol. Surv. Vict.*, Bull. 52, 1929 : 35.

III. Metamorphic Gneiss. Little River, Ensay. Anal. A. W. Howitt. *Proc. Roy. Soc. Vict.*, 22, 1886 : 75.

IV. Mica-schist. Hinnunjii Morass, Omeo. Ibid., 24 : 107. Anal. A. W. Howitt.

V. Average Normal Pelite (11 analyses). See Table 1. As the ratio of FeO/Fe$_2$O$_3$ varies with the degree of metamorphism, total ferric oxide is given in the average.

possibly derived. The xenolith has undoubtedly been influenced by reaction with the magma and is not solely the product of pyrometamorphism. As iron oxides, alumina and magnesia are higher in the xenolith than in the average pelite, there appears to have been some selective reaction and a storing up of these constituents within the xenolith. This may be accounted for by assuming that certain minerals lower in the reaction series than those being precipitated by the magma were dissolved out, thereby enriching the xenolith in phases higher in the reaction series and not so readily assimilated by the magma.

The knotted schists of the andalusite-zone at Cooma (Joplin, 1942) were believed to have formed as a contact-zone about the Cooma gneiss, and the knotted schists of the Albury region probably bear a similar relation to the igneous material. Thus it cannot be assumed that the knotted schists were already formed and completely stable at the time of their immersion by the magma, but it is not unreasonable to assume that some segregation of chlorite and of iron ores had already taken place as the magma worked its way up beneath the sediments and subjected them to a gradually increasing temperature. Such an early spotting is a common feature of normal contact-zones and may take place well outside the hornfels zone at some distance from the igneous body. Such clots of chlorite (probably with some sericite) were undoubtedly surrounded by a base very similar in composition to the aggregate surrounding the "knots" of the more highly-
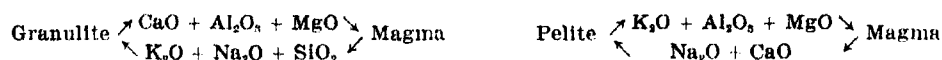
developed knotted schists and referred to by Tattam (1929) as a two-mica base. It has already been stated that the psammopelite is the most common type of sediment in this district, and these rocks contain varying amounts of quartz associated with the micas of the base. Thus the base of these rocks, at the time of the invasion of the granite, probably consisted of quartz, sericite and a little chlorite. These minerals being low in the reaction-series would dissolve in the magma (Type I, Nockolds, 1933), leaving the incipient knots or any chlorite-rich bands that might have been present in the psammopelite. Subsequently these solid bodies, rich in alumina, magnesia and iron oxides, were altered by pyrometamorphism to give cordierite-spinel-sillimanite assemblages (see Equations, p. 112).

Reference to Table 10 suggests that the xenolith has gained soda and lime from the magma and has probably contributed potash. Although the analysis of the xenolith shows high alumina and magnesia there is little doubt that small quantities of both have been added to the magma, this being masked by the storing up of these constituents within the xenolith. Most of the magnesia and alumina added to the magma, however, would have been derived from the lower phase minerals of the base.

The more siliceous types of psammopelite suffered a similar disintegration by the solution of the low-grade minerals, but in this case there was sufficient silica present in the incipient spots to give rise to garnet under the appropriate conditions of pyrometamorphism.

Thus both granulites and pelites have contributed towards the contamination of the magma. This has been brought about first by a solution of the lower phase minerals and an accompanying mechanical disintegration and segregation of the constituents of higher melting-point and later by reciprocal reaction between the magma and undissolved xenoliths, the latter in the meantime having been subjected to pyrometamorphism.

The chemical effects of the contamination process may be represented diagrammatically thus:

$$\text{Granulite} \nearrow \begin{array}{c} CaO + Al_2O_3 + MgO \searrow \\ K_2O + Na_2O + SiO_2 \nearrow \end{array} \text{Magma} \qquad \text{Pelite} \nearrow \begin{array}{c} K_2O + Al_2O_3 + MgO \searrow \\ Na_2O + CaO \nearrow \end{array} \text{Magma}$$

iv. *Chemical Discussion.*

Apart from the two contaminated gneisses at present under discussion the only other Ordovician igneous rocks of this area are the oligoclase granites and the pegmatites described above. Of these the first are the more abundant, and form the larger sills, so it is not unreasonable to assume that it was a magma of this type which became contaminated to form the cordierite-bearing gneiss.

Although the calculation of a theoretical analysis is highly speculative, there is good evidence to show that contamination has taken place and that both basic granulites and pelites have played their part in bringing it about. Reference to Table 6 will show that the oligoclase granites, which possibly represent the parent magma, contain much less lime than the cordierite-bearing gneiss (Table 8), and to calculate a theoretical rock of this composition, it is necessary to add both granulite and pelite as presupposed in the above discussion and supported by the petrographical evidence. This could have been done in a single step, as was probably the case in nature, but to facilitate calculation and to explain each step of the process, two parts of oligoclase granite are first mixed with one part of the granulite and then two parts of this mixture are added to one part of the base of the pelite. This means that four parts of magma react with three parts of country-rock, and it is thus necessary to postulate a large underlying magma chamber, the present surface exposures representing only the roof. Unfortunately the writer has not analysed the mica-quartz base of the psammopelites which are so common in the Albury district; and the calculation has therefore been made on Tattam's analysis of a two-mica base, a type evidently free from quartz, and this has been re-calculated after adding sufficient silica to make it comparable with that of the cordierite-bearing gneiss (Table 11). Thus the actual amount of silica has been assumed, but the resultant analysis (VI) when compared with the actual analysis of the gneiss (VII) shows a fairly close parallelism, and though oxides are not identical in the two analyses, they are of the right order, and better results might easily have

been obtained from other analyses of the same rock-types as these show small variations among themselves as the tables throughout this communication tend to show.

TABLE 11.

			I.	II.	III.	IV.	V.	VI.	VII.
SiO$_2$ ..	..	..	73·99	52·23	67·09	48·80	57·94	66·94	66·94
Al$_2$O$_3$	..	..	16·08	22·16	18·20	25·20	21·70	18·06	16·65
Fe$_2$O$_3$	..	..	0·65	0·72	3·84	4·00	6·25	5·20	0·40
FeO ..	..	..	—	8·50	—	4·20	—	—	4·77
MgO	..	..	0·31	4·75	1·80	3·82	2·80	2·32	2·19
CaO ..	..	..	0·09	7·29	2·50	0·45	1·32	1·09	0·94
Na$_2$O	..	..	3·67	0·43	2·60	0·96	1·78	1·48	2·11
K$_2$O ..	..	..	4·04	1·70	3·28	6·75	5·01	4·17	3·56
H$_2$O ..	..	..	0·51	0·74	—	4·78	....	—	2·25
TiO$_2$	..	..	abs.	0·76	0·25	1·16	0·72	0·59	0·60
P$_2$O$_5$ ..	..	..	0·43	0·46	0·44	....	0·15	0·12	0·01
MnO ..	..	..	tr.	0·11	—	0·09	0·03	0·03	0·06
			99·77	99·85	100·00	100·21	97·70	100·00	100·48

I. Oligoclase-microcline Granite. See Table 6.
II. Pyroxene-granulite. See Table 4.
III. Calculated analysis consisting of two parts of I and one part of II.
IV. Two-mica base, Knotted Schist. Anal. C. M. Tattam. *Geol. Surv. Vict.*, Bull. 52, 1929 ; 35.
V. Calculated analysis consisting of two parts of III and one part of IV.
VI. Analysis V re-calculated as explained in text.
VII. The Cordierite-bearing Gneiss. See Table 8.
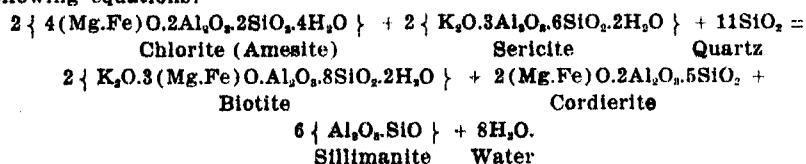
v. *Mineral Transformations.*

In the above discussion on the contamination of the gneiss, it was suggested that the silica-poor assemblages arose either from spots representing the incipient knots of the knotted schists or from very restricted chlorite-rich bands in the psammopelites.

Before pyrometamorphism occurred, therefore, it must be assumed that such spots or seams have been isolated from their more siliceous lower melting-point base by solution in the magma. The solid, insoluble material has been strewn about in the magma, therefore, to form the minute silica-poor xenoliths which are not very apparent in handspecimen but which appear so numerous under the microscope.

Mineral transformations due to pyrometamorphism, or very high-grade thermal metamorphism due to immersion, will first be considered with regard to the pelitic xenoliths and then reaction changes will be dealt with. As no very noteworthy changes take place during the pyrometamorphism and subsequent assimilation of the basic granulites, these will not be considered.
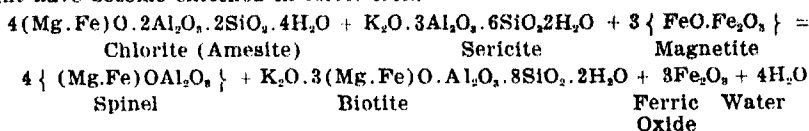
(a). *Pyrometamorphism.*—At the time of immersion, the incipient spots in the schists probably consisted mainly of chlorite, iron ores and sericite, and the commonest high-grade assemblage consists of cordierite, sillimanite, iron-rich biotite and spinel.

It is probable that a very small quantity of quartz remained in the "knot" after its immersion and this would have been used in converting chlorite and sericite into cordierite, sillimanite and biotite. Unfortunately the chemical composition of this chlorite is unknown, but as the analyses of a number of pelites are available, it is assumed that it contained both magnesia and alumina, probably with a greater preponderance of alumina, so amesite is considered to be a likely composition and is used in the following equations:

$$2 \{ 4(Mg.Fe)O.2Al_2O_3.2SiO_2.4H_2O \} + 2 \{ K_2O.3Al_2O_3.6SiO_2.2H_2O \} + 11SiO_2 =$$

Chlorite (Amesite)   Sericite   Quartz

$$2 \{ K_2O.3(Mg.Fe)O.Al_2O_3.8SiO_2.2H_2O \} + 2(Mg.Fe)O.2Al_2O_3.5SiO_2 +$$

Biotite   Cordierite

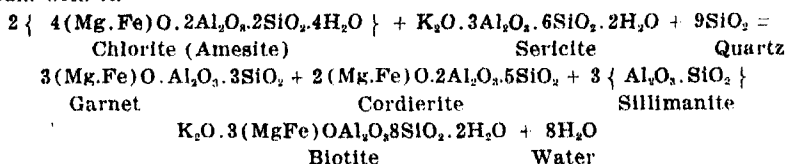$$6 \{ Al_2O_3.SiO \} + 8H_2O.$$

Sillimanite   Water

When no further silica was available the remaining chlorite and sericite would react with magnetite to form an iron-rich spinel. It was noted in the petrography that spinel often formed rims around the granules of magnetite. Ferric oxide probably passed out

to the magma, this oxide being very mobile as the formation of skarns has shown. Biotite again arises as a result of this reaction, and though not shown in the equation, it might have become enriched in ferric iron.
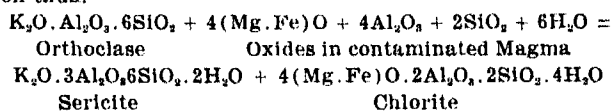
$$4(Mg.Fe)O.2Al_2O_3.2SiO_2.4H_2O + K_2O.3Al_2O_3.6SiO_2 2H_2O + 3 \{ FeO.Fe_2O_3 \} =$$
Chlorite (Amesite)   Sericite   Magnetite

$$4\{ (Mg.Fe)OAl_2O_3 \} + K_2O.3(Mg.Fe)O.Al_2O_3.8SiO_2.2H_2O + 3Fe_2O_3 + 4H_2O$$
Spinel   Biotite   Ferric   Water
Oxide

In the spinel the ratio Mg/Fe is 1/7, and it has been taken as 1/1 in the other minerals.

Among the silica-rich pelite xenoliths the most common type is the garnet-cordierite-sillimanite-biotite assemblage, sillimanite usually clouding the garnet even when it is not present as a normal constituent in the body of the rock. In these rocks the quartz has been more abundant in the knots and seams and has either been "armoured" by the other minerals, and therefore incapable of being removed by solution, or the schists have been immersed in the magma at a time when quartz was already in phasal equilibrium with it.
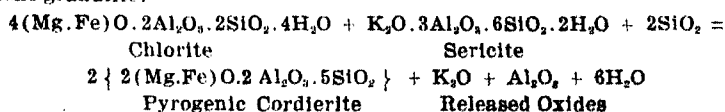
$$2\{ 4(Mg.Fe)O.2Al_2O_3.2SiO_2.4H_2O \} + K_2O.3Al_2O_3.6SiO_2.2H_2O + 9SiO_2 =$$
Chlorite (Amesite)   Sericite   Quartz

$$3(Mg.Fe)O.Al_2O_3.3SiO_2 + 2(Mg.Fe)O.2Al_2O_3.5SiO_2 + 3\{ Al_2O_3.SiO_2 \}$$
Garnet   Cordierite   Sillimanite

$$K_2O.3(MgFe)OAl_2O_3 8SiO_2.2H_2O + 8H_2O$$
Biotite   Water

(b). *Reaction.*—As quartz, sericite and a little chlorite actually dissolve in the magma at an early stage in the assimilation process, their constituent elements become available for the formation of other minerals, so it is not necessary to use the formulae of any of these minerals on the magmatic side of the following equations.
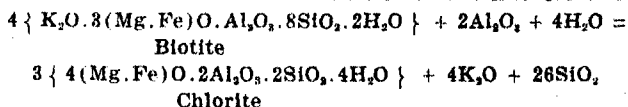
It was noted above that orthoclase was being precipitated when the magma was contaminated and that it was subsequently altered to chlorite and sericite as a result of the contamination thus:

$$K_2O.Al_2O_3.6SiO_2 + 4(Mg.Fe)O + 4Al_2O_3 + 2SiO_2 + 6H_2O =$$
Orthoclase   Oxides in contaminated Magma

$$K_2O.3Al_2O_3 6SiO_2.2H_2O + 4(Mg.Fe)O.2Al_2O_3.2SiO_2.4H_2O$$
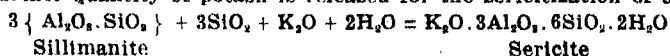Sericite   Chlorite

After the high-grade metamorphism of the pelites these too suffer reaction, sillimanite being converted into sericite, and cordierite to a mixture of chlorite and sericite. For these changes to have been brought about, potash must have been added by the magma, though it was shown above that potash was originally derived from the schist in the form of sericite. At this late stage, however, the magma has begun to precipitate pyrogenic cordierite, thus binding part of the alumina of the original sericite with magnesia and setting free its potash. Obviously a quantity of both magnesia and alumina would have been made available earlier by the solution of, and reaction with, the pyroxene-granulite:
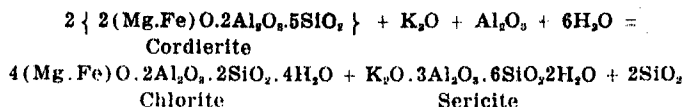
$$4(Mg.Fe)O.2Al_2O_3.2SiO_2.4H_2O + K_2O.3Al_2O_3.6SiO_2.2H_2O + 2SiO_2 =$$
Chlorite   Sericite

$$2\{ 2(Mg.Fe)O.2 Al_2O_3.5SiO_2 \} + K_2O + Al_2O_3 + 6H_2O$$
Pyrogenic Cordierite   Released Oxides

The available alumina is used for the conversion of biotite into chlorite:

$$4\{ K_2O.3(Mg.Fe)O.Al_2O_3.8SiO_2 2H_2O \} + 2Al_2O_3 + 4H_2O =$$
Biotite

$$3\{ 4(Mg.Fe)O.2Al_2O_3.2SiO_2.4H_2O \} + 4K_2O + 26SiO_2$$
Chlorite

Thereby a further quantity of potash is released for the sericitization of sillimanite:

$$3\{ Al_2O_3.SiO_2 \} + 3SiO_2 + K_2O + 2H_2O = K_2O.3Al_2O_3.6SiO_2.2H_2O$$
Sillimanite   Sericite

Cordierite, in both xenolith and contaminated igneous rock, is made over into a mixture of chlorite and sericite which is a reversal of the equation showing the genesis of pyrogenic cordierite:

$$2 \{ 2(Mg.Fe)O.2Al_2O_3.5SiO_2 \} + K_2O + Al_2O_3 + 6H_2O =$$
Cordierite
$$4(Mg.Fe)O.2Al_2O_3.2SiO_2.4H_2O + K_2O.3Al_2O_3.6SiO_2 2H_2O + 2SiO_2$$
Chlorite　　　　　　　　　　Sericite

These reactions continue until equilibrium is set up and the pelitic xenolith consists entirely of a mass of chlorite and sericite, or until the magma has cooled to such an extent that further reaction is impossible. Thus all stages in the reaction process are to be found among the numerous, minute pelitic xenoliths.

(b). Two-Mica Gneisses.

The Albury or two-mica gneiss crops out on the Howlong Road, on the northern bank of the Murray River, just below Monument Hill, the main outcrop probably being in Victoria. Good exposures of the gneiss may be seen in the Municipal Quarry and in the road cuttings between the western end of Smollett Street and West Albury Post Office.

A rather similar type of gneiss occurs about 10 miles from Jingellic on the Tumbarumba Road, and a slightly different, though closely related type, occurs just north of Womargama on the Holbrook Road.

At the intersection of the roads, Pors. 107/112, Parish of Albury, just south of the Roman Catholic Orphanage, several tors and a weathered exposure in the road cutting suggest the presence of an igneous rock. Large pink felspars, often up to an inch across, are common and the weathered mass is threaded with veins of pegmatite. This occurrence suggests the Albury gneiss, but closer examination discloses the fact that it is a highly-granitized schist, and its relation to the Albury gneiss is discussed below.

1. Xenoliths and Granitized Schists.

An examination of the altered sediments on Monument Hill, in the immediate vicinity of the Albury gneiss, indicates that they are mainly psammites and psammopelites. Very good exposures of these may be seen in a quarry on the western side of the hill overlooking West Albury. At this locality the sediments are unaffected by granitization and the pelitic sediments occur only as very narrow bands in a great thickness of psammite and banded psammopelite not unlike the corduroy granulite of Cooma.

In the Municipal Quarry on the Howlong Road the gneiss is seen to be crowded with xenoliths in all stages of disintegration. Pelites are mainly represented by highly-micaceous patches and the less pelitic types by granulites and banded granulites. The latter usually form the larger inclusions which show little evidence of assimilation. Small xenoliths of granulite are not so evident as small fragments of pelite and were apparently more digestible just as the basic granulite was more digestible in the cordierite-bearing gneiss. The large unassimilated masses of granulite were probably caught up at a late stage in the cooling history, but even at this stage the more schistose pelite was capable of being split up by mechanical disintegration and was no doubt already a mica-schist. Furthermore, the pelites occurred only as fairly narrow seams in the granulites, so at an earlier stage, when the granulite was capable of being assimilated, the thin rafts of micaceous schist were probably in equilibrium with the magma and remained as mica clots.

In describing the granitized schists it has been pointed out (p. 96) that the psammites and more psammitic psammopelites are usually affected by felspathization, and this process is significant in considering the origin of the two-mica gneiss.

(a). Psammites and Psammopelites.—In handspecimen these do not appear to have suffered an advanced stage of alteration, although some types do show obvious felspathization.

Under the microscope all stages between the slightly granitized psammite and the completely soaked and resorbed fragment can be discerned. The least altered types consist of a granoblastic aggregate of quartz, muscovite and red-brown mica and the grainsize varies from 1–2 mm. The more pelitic varieties contain aggregates of the two micas which form wisps or wide swirls and sinuous streaks through the rock, indicating an earlier plication. Quartz and muscovite often contain needles of sillimanite. Zircons
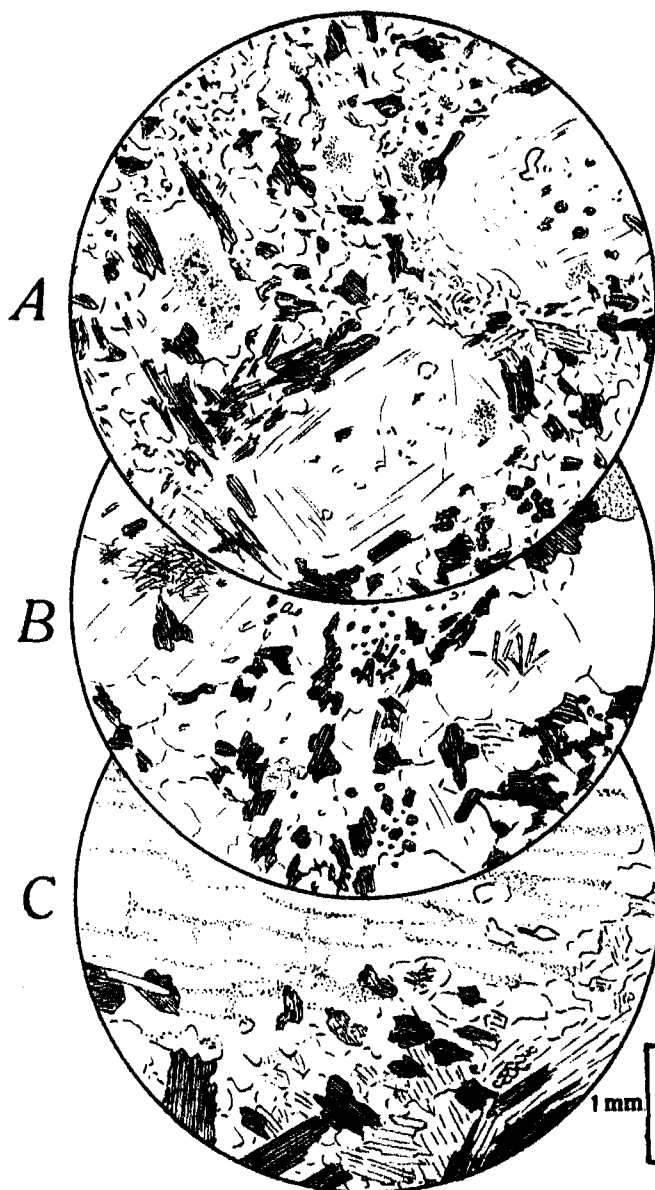
Fig. 7.

A. Granitized schist showing large "phenocrysts" of oligoclase in psammite consisting of a granoblastic aggregate of quartz, biotite, muscovite and altered orthoclase. A little tourmaline is present in the NE. quadrant.

Ten miles north of Jingellic on the Tumbarumba Road.   × 16.

B. Large quartz, plagioclase and orthoclase grains wedged into schist consisting of biotite, cordierite, quartz, orthoclase and sillimanite. The plagioclase at the left of the figure and the quartz at the right have enveloped masses of sillimanite.

Near the Orphanage, Albury.   × 16.

C. Two-mica gneiss showing portion of large grain of microcline and long blade-like crystals of biotite and muscovite developing in a fine granoblastic mass of quartz and greisenized felspar.

Municipal Quarry, Albury.   × 16.

are commonly present in the biotite. Felspathization is usually marked by the development of large plagioclase felspars which are wedged in among the original minerals of the psammite (Fig. 7, A).

(b). *Pelites.*—These are much altered, and although andalusite, cordierite and sillimanite sometimes occur, they are more often completely altered into an aggregate of micas—mainly muscovite and green mica crammed with rutile needles. The latter possibly represents the breakdown of an earlier red biotite which had now reached a state of equilibrium with, but has not been completely resorbed by, the magma.

ii. *The Gneiss.*

As exposed in the Municipal Quarry, the Albury gneiss is a light grey rock containing much mica and rounded masses of quartz and pink phenocrysts of felspar up to about 1½ inches across. In handspecimen it is extremely like the Cooma gneiss. The mass is cut by many dykes and veins of pegmatite and schorl, and sometimes by veins of pure tourmaline. As stated above, xenoliths are numerous.

The two-mica gneisses near Woomargama and on the Tumbarumba Road are very similar.

The granitized schist near the Orphanage is an excellent example of an intermediate step between granitized schist and gneiss. In the field it appears to be an outcrop of an igneous rock, but under the microscope it is revealed as a granitized schist consisting of andalusite, sillimanite, cordierite, muscovite, red-brown biotite and striated orthoclase. The orthoclase may form bands indicating a gneissic structure and the rock is rather suggestive of the coarser types of mottled gneiss from the permeation-zone of Cooma. This rock has obviously been soaked by "granitic fluid" and large units of orthoclase, oligoclase ($Ab_{72}An_{28}$) and quartz have wedged apart the schist and enveloped some of its minerals. Needles of sillimanite are commonly present in the newly formed plagioclase (Fig. 7, B).

Specimens from the Municipal Quarry showing no obvious xenoliths in handspecimen mark a further stage in the resorption and granitization of the psammopelitic material, but no specimen has been examined in which original sedimentary quartz, orthoclase and micas have not been identified among the later developed larger grains of oligoclase, microcline, quartz and micas of igneous origin. The original biotite is often chloritized or bleached and the felspar completely replaced by muscovite, and it is sometimes difficult to identify these in between the larger blades of magmatic muscovite and chocolate-brown biotite (Fig. 7, C). That part of the muscovite that has an igneous origin is not infrequently plumose in its development. This type is very similar to the muscovite-rich phase of the Cooma gneiss (Joplin, 1942, p. 187) which was noted as occurring in isolated outcrops among the granitized schists. It is now considered that the Cooma rock developed in the same way as that suggested for the Albury gneiss. In the normal phases of the Cooma gneiss, however, pink pleochroic andalusite is a typical constituent and this is fairly rare in the Albury gneiss which compares more closely to the muscovite-rich phase at Cooma. The difference is probably a matter of volatiles, particularly of water content in the invaded rocks and in the intrusive magma.

A microscopic study of the Albury gneiss reveals a definite tendency towards mantling, and it is of interest to note that most of the large "phenocrysts" are composite bodies. They consist either of microcline, often albitized, or of oligoclase, and these enclose partly resorbed grains of orthoclase, sometimes mantled by a more basic plagioclase, as well as independent crystals of the more basic plagioclase. The development of oligoclase about orthoclase recalls some of the features of the Finnish rapikivi granites (Wahl, 1925; Sederholm, 1928), for though not a true rapikivi texture it is closely allied to it. In the rapikivi granites the orthoclase grains are usually rounded and the mantling plagioclase is in parallel intergrowth with them. In the Albury rocks, however, the orthoclase shows a more irregular resorption, and though these incompletely resorbed fragments may be in optical continuity with one another, they are not necessarily in parallel intergrowth with the mantling oligoclase (Fig. 8). Furthermore, the partly resorbed orthoclase may be mantled with microcline, or by a more basic plagioclase before being included in either microcline or oligoclase. When the basic

plagioclase forms independent crystals the mantling oligoclase is often in parallel intergrowth with them and this gives the oligoclase a peculiar checked appearance. Orthoclase often shows marginal alteration to myrmekite.
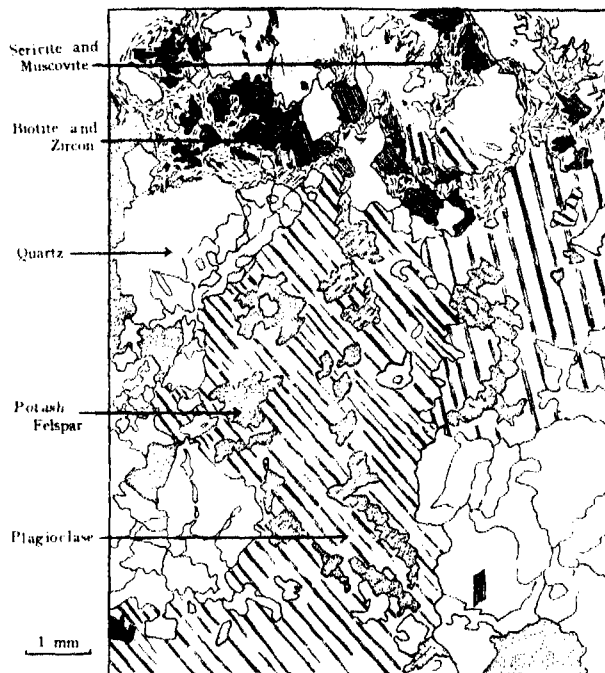

Fig. 8.—Composite unit occurring as a "phenocryst" in the two-mica gneiss.

iii. *The Contamination Process.*

In discussing the rocks of the permeation—or sillimanite—zone at Cooma (Joplin, 1942), it was shown that orthoclase developed as the result of high-grade metamorphism; and although this zone cannot be traced at Albury, there is some evidence of its existence prior to the heavy greisenization caused by the numerous sills which invaded this zone. Thus it can be assumed that the high-grade rocks, before they were granitized, contained varying amounts of orthoclase felspar. The granitized schist near the Orphanage gives further corroboration of this.

The largest sills of the district consist of oligoclase-granite and, as in the case of the cordierite-bearing gneiss, it is assumed that this magma type was responsible for the granitization. The schists were actually soaked in the quartz-felspar magma, and since the psammites and psammopelites consisted largely of quartz, it would probably represent a phase lower in the reaction series than those being precipitated by the magma. The orthoclase of the schists tended to be resorbed, but before this process was complete, magmatic material was deposited in the interstices of the partly disintegrated xenolith. Thus plagioclase of a slightly basic type was first deposited by the magma either enveloping the partly resorbed orthoclase or as independent small crystals. As the crystallization of the magma continued, a more acid plagioclase mantled these as well as an occasional grain of original quartz which had failed to go into solution. Microcline and quartz were also deposited from the magma at about this time and thus early magmatic minerals and partly resorbed sedimentary ones are characterized by mantling.

Thus there are all stages between the partly granitized or felspathized psammopelite and the most completely stabilized type, which in handspecimen closely resembles a true porphyritic igneous rock. As the psammopelites are not so far removed in mineral composition from the granites themselves, there is no very marked evidence of reciprocal

reaction, and the contamination process has been due partly to a solution of the constituents low in the reaction series, and partly to mechanical disintegration of the xenolith brought about by both dissolution and by the wedging in of large grains of quartz and felspar.

iv. *Chemical Discussion.*

Again, any attempt to calculate a theoretical analysis must be highly speculative and must presuppose a large underlying magma chamber of oligoclase granite, but it has been shown in the petrography that it is possible to trace almost every step in the granitization of the psammopelite through to the formation of the contaminated gneiss and the writer is emboldened to attempt such calculations. Unfortunately no analyses have been made of the psammopelites of the Albury district, but there are available types, which are believed to be similar, from the Victorian part of the complex and from Cooma. Table 12 shows analyses of both actual and theoretical gneiss, and it can be seen that by mixing various quantities of psammopelite and oligoclase granite from these areas it is possible to calculate the analyses of rocks whose compositions closely resemble the two-mica gneiss type. In doing this, care was taken to choose pairs of analyses from the same locality in each case, and thus there is no theoretical gneiss for the Albury district itself.

TABLE 12.

			I.	II.	III.	IV.	V.	VI.	VII.
SiO₂	..	..	70·44	71·93	69·79	70·65	72·44	69·14	69·79
Al₂O₃	..	..	15·84	14·62	16·47	15·25	14·72	18·04	16·81
Fe₂O₃	..	..	0·53	0·83	0·53	0·83 ⎫	2·41	2·40	3·65
FeO	..	..	3·35	2·25	2·97	3·45 ⎭			
MgO	..	..	1·24	1·18	1·95	1·63	1·21	1·32	1·50
CaO	..	..	0·73	0·91	0·73	0·94	0·57	0·52	0·73
Na₂O	..	..	1·70	1·98	1·68	1·77	2·14	2·09	1·65
K₂O	..	..	4·09	5·03	3·44	4·63	4·56	4·83	4·09
H₂O+	..	..	0·62	0·75	0·99	0·60 ⎫	1·22	1·15	0·91
H₂O−	.	..	0·09	0·34	0·49	0·00 ⎭			
TiO₂	..	..	0·66	0·33	—	0·65	0·59	0·44	0·63
P₂O₅	..	..	0·22	0·22	0·06	0·12	0·14	0·07	0·20
MnO	..	..	tr.	0·03		0·05	—	—	0·04
BaO	..	..	—	0·02	..	..	..	..	—
			99·51	100·42	99·10	100·66	100·00	100·00	100·00
Sp. Gr.	..	..	2·74	—	2·72	2·79	..	—	2·70

I. Albury Gneiss. Municipal Quarry, Howlong Road, base of Monument Hill. Anal. G. A. Joplin.

II. Granite. Mt. Wagra, North-eastern Victoria. Anal. C. M. Tattam. *Geol. Surv. Vict.*, Bull. 52, 1929: 38.

III. Slightly foliated Granite. Wilson's Creek, Omeo. Anal. A. W. Howitt. *Trans. Roy. Soc. Vict.*, 24, 1887.

IV. Cooma Gneiss. Massie Street, Cooma. Anal. G. A. Joplin. PROC. LINN. SOC. N.S.W., 67, 1942: 188.

V. Equal parts of Cordierite Hornfels (Anal. 8) and Quartz-felspar injection type (Anal. 24). Both analyses from C. M. Tattam. *Geol. Surv. Vict.*, Bull. 52, 1929: 36 and 38.

VI. Equal parts of Hornfels (Orr's Gully, A. W. Howitt, see Table 3) and Muscovite-granite (Omeo, A. W. Howitt, see Table 6, this communication).

VII. Two parts of Corduroy Granulite (Anal. III. PROC. LINN. SOC. N.S.W., 67, 1942: 168) and one part of Albite-muscovite Gneiss (Cooma, see Table 6, this communication).

The Woomargama gneiss is on the northern edge of the area mapped and has not been examined very carefully, but in handspecimen it is identical with the Albury gneiss, and on approaching it from the west, a zone of biotite schists, a zone of knotted schists and a zone of granitized schists were traversed, as in the case of the Ordovician two-mica gneisses elsewhere. It is assumed that it has a somewhat similar origin, though the chemical composition suggests that the assimilated material may have been more basic. Low-grade psammopelites with a tuffaceous matrix have been noted on the road opposite the T.S.R., just south of Woomargama, and the fact that this rock is comparable to the theoretical type calculated by mixing oligoclase-microcline granite and pyroxene-granulite may have some significance.

TABLE 13.

					I.	II.
SiO$_2$	..	..	..	..	66·43	67·09
Al$_2$O$_3$	..	..	..	..	17·53	18·20
Fe$_2$O$_3$	..	..	..	..	0·15⎫	3·84
FeO	..	..	..	..	3·76⎭	
MgO	..	..	..	..	1·91	1·80
CaO	..	..	..	..	2·55	2·50
Na$_2$O	..	..	..	..	2·37	2·60
K$_2$O	..	..	..	..	3·22	3·28
H$_2$O +	..	..	..	..	0·61	—
H$_2$O —	..	..	..	..	0·21	—
TiO$_2$	..	..	..	..	1·10	·0·25
P$_2$O$_5$	..	..	..	..	0·07	0·44
MnO	..	..	..	..	—	—
					99·91	100·00

I. Two-mica Gneiss. Por. 204, Par. of Woomargama.
Anal. G. A. Joplin.
II. Theoretical Gneiss. See Table 11, Anal. III.

3. THE LEVEL OF THE INTRUSIONS.

It is obvious from the foregoing discussion that the type of metamorphism and the nature of the rocks involved in it are closely comparable in the Albury and Cooma districts; but, as indicated in the section of this paper dealing with the metamorphic zones (p. 90), the zones at Cooma are more sharply defined and there is no zone of sills to complicate the higher grade zones as in the Albury region. Furthermore, although a later granite occurs at Cooma, it is well away from the main centre of Ordovician metamorphism, and did not interfere with it, whilst between Albury and Jingellic the contact-zones of the later granite often obscure the high-grade zones of Ordovician metamorphism. Nevertheless, these high-grade zones do not appear to have been so well developed in the Albury area. Again, the Cooma Complex could be distinguished as a complete unit in itself, whilst the area examined on the northern bank of the Murray represents only the northern fringe of the great complex of North-eastern Victoria.

Nevertheless, the apparently more restricted development of the high-grade zones, together with the great development of sills at Albury, suggests that this area represents a higher level in the complex as compared to that of Cooma. The fact that it was possible to trace the various stages in the development of the gneiss by the granitization and assimilation of the sediments also points to the magma's having cooled at a higher level where chemical and mineralogical changes had not had time to become completely stabilized.

It is likely, however, that several levels are represented within the Victorian Complex and studies further south may reveal that the main mass was more deep-seated and that the Albury area represents only the uppermost margin of the Ordovician intrusions.

IV. THE POST-ORDOVICIAN INTRUSIVES.

In the present paper these rocks are not studied in detail, but reference must be made to them as they have engulfed great areas of the Ordovician schists and have superimposed their contact effects upon them.

1. THE INTRUSIVE ROCKS.

At Mullanjandra, a mass of sheared gneiss or porphyry strikes about N. 50° W. across the main road, where it is covered by the alluvium of Mullanjandra Creek, but elsewhere forms a ridge of prominent hills. The full extent of the outcrop has not been mapped, but it is at least 6 miles in length and up to 1½ miles in width. A little faulting has possibly occurred in the region of Mullanjandra Creek (see Plate xv).

In handspecimen this rock bears a striking resemblance to the white gneiss of Cooma (Browne, 1914, 1943; Joplin, 1943) to which Browne has assigned a Silurian age.

Nowhere have very satisfactory contacts been observed but it appears to invade the Ordovician schists and the porphyries which are unconformable with them. Slates interbedded with the porphyries appear to be silicified along the creek in Por. 158, Par. of Mullanjandra, and as this is only a short distance from the gneiss, it is likely that it is responsible for the silicification. It has been suggested that the porphyries are of Lower Devonian age, but this must still remain an open question, for even though they may be silicified by the gneiss, it has been assigned a Silurian age only upon a lithological resemblance.

Even-grained and porphyritic granites, associated with large masses of granite-porphyry, are very numerous along the northern bank of the Murray at intervals between Wymah and Jingellic and probably occur in much of the mountainous country to the north. To the north of Albury there is a large area of granite, partly covered by soil and alluvium near Jindera, and this extends east to Table Top (Plate xv).

It is likely that granites of several ages are represented among these outcrops.

A porphyritic granite showing a marked parallelism of the phenocrysts occurs just east of Jingellic on the Tooma Road and the same type crops out on the Tumbarumba Road about 10 miles from Jingellic, and about 9 miles north of the outcrop on the Tooma Road. The relation between these two outcrops has not been studied but it is likely that they are continuous and boulders in the eastern tributaries of Horse Creek suggest that the hills to the east are composed of this rock-type. This rock may possibly be of Silurian age.

The Jindera granite, briefly described in an earlier communication (Joplin, 1944), is also porphyritic, but shows no directional structures and is very similar to types occurring near Dora Dora and Talmalmo, where large masses of granite-porphyry also occur.

The Hawksview granite, also previously described, is a massive two-mica granite with a very occasional phenocryst of orthoclase, and is particularly rich in white mica. It shows very sharp contacts against the cordierite-bearing gneiss and is obviously of much later origin.

Howitt (1887) has described a porphyritic granite from Omeo, which, except for its higher MgO, is rather similar to the Hawksview granite in chemical composition. Howitt has stated that in the field the porphyritic granite is closely related to a foliated type, and quotes analyses of both. The foliated type is obviously related to the two-mica gneisses with which it is compared in Table 12. Concerning the relation of the porphyritic and foliated granites at Omeo, Howitt concludes: "for the present I must leave this in a state of doubt". The present writer's experience on the Upper Murray, however, leads her to the conclusion that the porphyritic granite of Omeo is probably much later and has invaded the earlier two-mica gneiss which is intimately related to the Ordovician schists.

In the earlier paper (Joplin, 1944), it was suggested that the two-mica granite at Run Boundary occurred as an Ordovician sill, but a more detailed petrological and chemical examination has shown that it bears no relation to the other sills of the area, and, though apparently a concordant intrusion, is possibly of later origin. In Table 14 the analysis of this rock is compared with the Corryong granite and it is interesting to note that Edwards (1937) has said: "outcrops of the granite salients are more or less linear and parallel to the strike of the invaded Ordovician".

As these granites have not been studied in detail, it is not fitting to discuss their relative ages, but there certainly seems to be several periods of igneous intrusion represented, possibly Silurian, Middle Devonian and Kanimbla, and the problem would well repay a more detailed study. Edwards has made a detailed study of the Corryong and Pine Hill granites and considers that they are of two ages—both post-Ordovician. In discussing this he says: "If the orogony can be regarded as Lower Devonian in age, then the Corryong granite may be post-Lower Devonian, whilst the Red granite series may coincide with a Middle or Upper Devonian minor orogony. If the Corryong granite, on the other hand, is post-Middle Devonian, the Red granite series cannot be older than Lower Carboniferous and may be much younger."

Although MgO is higher in the Corryong granite, it bears some chemical relation
to the Run Boundary and Koetong granites with which it is compared in Table 14,
whilst the Hawkesview granite, with its lower CaO and Na₂O and higher K₂O, seems
to be more closely related to the porphyritic granite of Omeo, though here again there
is a discrepancy in the MgO content. Edwards (1937) has shown that the later types,
of which the Pine Mt. granite is a representative, also contain high K₂O, but as these
have a very much higher silica content, they cannot readily be compared with the two
analyses in Table 15.

It is possible that detailed chemical work might show that these various granites
fall into groups, and this may be a means of distinguishing their relative ages.

TABLE 14.

	1.	II.	III.	IV.	V.	VI.
SiO₂	70·73	68·92	67·25	70·78	71·50	67·67
Al₂O₃	15·38	16·21	16·46	15·77	14·13	14·50
Fe₂O₃	0·50	0·57	0·42	0·69	0·60	0·87
FeO	2·31	2·42	1·99	2·44	3·23	3·78
MgO	0·79	1·04	1·00	0·72	1·17	2·21
CaO	2·54	2·31	2·74	2·53	2·70	2·18
Na₂O	3·78	2·43	2·91	2·88	2·97	2·38
K₂O	3·29	4·36	5·64	2·44	2·86	3·42
H₂O+	0·29	0·03	0·48	0·50	0·32	1·81
H₂O−	0·10	0·08	0·20	0·06	0·10	0·11
TiO₂	0·34	0·52	0·40	0·45	0·41	0·61
P₂O₅	0·42	0·30	0·19	0·25	0·35	tr.
MnO	0·04	0·03	0·02	0·08	tr.	—
Etc.	—	0·04	0·08	—	—	—
	100·51	100·16	99·78	99·59	100·34	99·54
Sp. Gr.	2·69	—	—	2·68	2·59	—

I. Two-mica Granite. Run Boundary Trigonometrical Station, Por. 244, Par. of Mungabarina, Albury district.
    Anal. G. A. Joplin.
II. Granite. Koetong Mass, Tallangatta-Granya Road. Anal. C. M. Tattam. *Geol. Surv. Vict.*, Bull. 52, 1929 : 38.
III. Granite. Osborne's Flat, Yackandandah Creek Basin. Anal. C. M. Tattam. Ibid.
IV. Biotite-granite. Moruya district. Anal. I. A. Brown. PROC. LINN. SOC. N.S.W., 53, 1928 : 160.
V. Granite. Enoggera, Queensland.
VI. Grey Biotite Granite. East of Lot 8, Section VII, near Contact. Par. of Cudgewa. Anal. F. F. Field. A. B.
    Edwards and J. G. Easton. *Proc. Roy. Soc. Vict.*, 50, 1937 : 82.

TABLE 15.

	I.	II.
SiO₂	69·71	68·87
Al₂O₃	17·90	16·62
Fe₂O₃	1·16	0·43
FeO	0·88	2·72
MgO	0·16	1·60
CaO	1·22	0·71
Na₂O	1·76	1·80
K₂O	6·14	6·48
H₂O+	0·73	0·74
H₂O−	0·04	0·21
TiO₂	0·34	—
P₂O₅	0·42	0·05
MnO	—	—
	100·46	100·23
Sp. Gr.	—	2·762

I. Two-mica Granite (Hawkesview Granite). Hume Weir
   Quarry, Por. 85, Par. of Thurgona. Anal. G. A. Joplin.
II. Porphyritic Granite. Wilson's Creek, Omeo. Anal. A. W.
    Howitt. *Trans. Roy. Soc. Vict.*, 24, 1887.
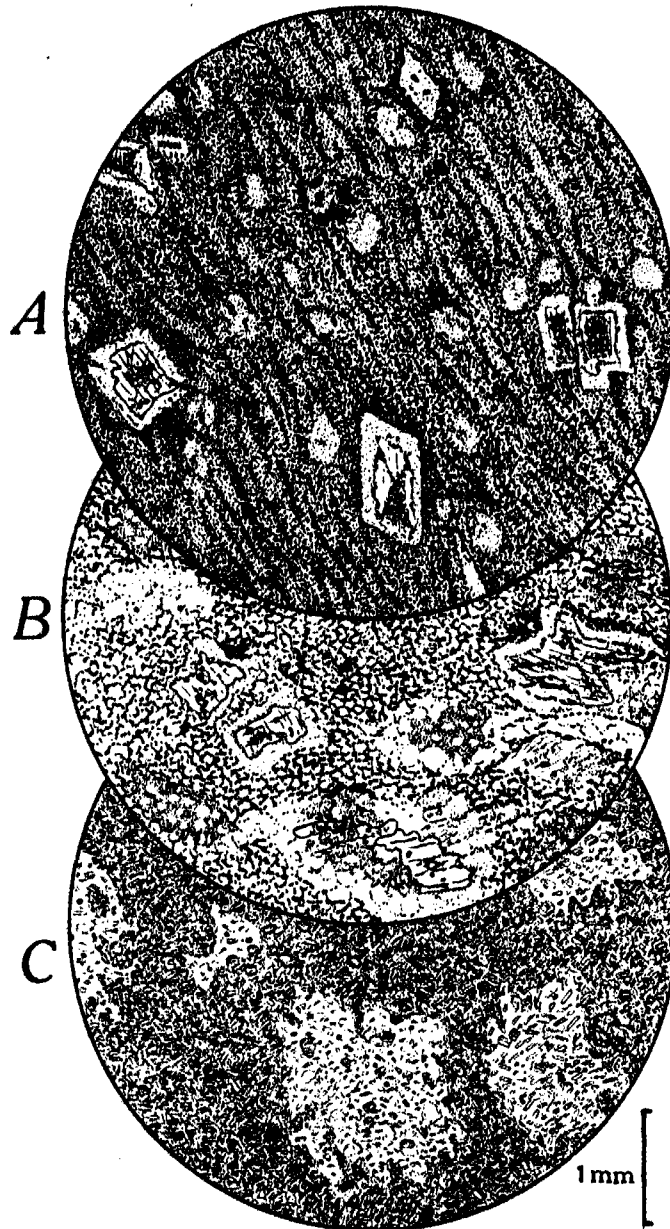
Fig. 9.—Hornfels in the aureoles of the younger granites.

A. Chiastolite-cordierite hornfels, about 1½ miles north of Jingellic, on the Tumbarumba Road. Small porphyroblasts of idioblastic chiastolite show a marginal alteration into sericite. Small porphyroblasts of cordierite are xenoblastic and completely altered. The base shows a marked schistosity and consists almost entirely of quartz and graphite. × 16.

B. A more advanced thermal alteration of the same rock-type from the roadside, 5 miles west of Jingellic, on the Albury Road. Porphyroblasts of andalusite (some chiastolite) and cordierite are much larger, and the base consists of a granoblastic mass of quartz and graphite, all traces of schistosity having been lost. × 16.

C. Cordierite hornfels from Burrumbuttock. Large irregular porphyroblasts of cordierite show sieve-structure. These occur in a fine base of biotite, muscovite, quartz and magnetite. × 16.

Obviously a great deal of work needs to be done on this problem, but it is outside the scope of this Ordovician study, and the present writer does not feel justified in spending further time on it.

2. THEIR CONTACT AUREOLES.

As mentioned above, the slates at the contact of the Mullanjandra gneiss appear to be silicified, but there is no hornfelsing.

In the neighbourhood of Jingellic, large spots consisting of radiating masses of chlorite suggest that a weak contact metamorphism has been superimposed on the zone of spotted schists. The chlorite "spots" show crystal boundaries suggesting that they are pseudomorphs after cordierite, and the change to chlorite is no doubt due to the low-grade contact effects of the (?) Silurian porphyritic granite on the Tooma Road, 3 miles east of Jingellic. This type of spotting can be followed almost up to the junction of the granite although the actual boundary is somewhat obscured. Furthermore, similar spotting is seen along Horse Creek, and this lends further support to the assumption that the porphyritic granite occurs in the hills to the east of this stream.

On the Tumbarumba Road, 2 miles from Jingellic, chiastolite and incipient cordierite are developed in the pelitic schists which were possibly in the biotite-zone of regional metamorphism (Fig. 9, A). At 10 yards from the granite on the Albury Road, 5 miles from Jingellic, this same rock-type has given rise to andalusite-cordierite hornfelses (Fig. 9, B).

Between Burrumbuttock and Jindera a large stretch of soil and alluvium probably covers granite. Small areas of granite crop out at intervals on the hills adjacent to the Ordovician schist, but the main evidence for the existence of a fairly extensive mass of granite lies in the fact that a contact aureole appears to occur between the schists and the alluvium. These hornfels are mainly cordierite-bearing types of which Fig. 9, C, is an example.

3. ASSOCIATED HYBRIDIZATION.

A sharp contact between the cordierite-bearing gneiss and Hawksview granite is exposed in the Weir Quarry, Por. 65, Parish of Thurgona, and large blocks of the gneiss frequently occur within the granite. The contacts of these xenoliths are usually very sharp and angular and remain so until an advanced stage in the hybridization process. Hybridization is noticeable particularly in the smaller blocks which first develop a marked gneissic banding. This seems to have been brought about by the development of new quartz and felspar about the quartz and felspar of the gneiss, and thus a faint original gneissic structure has become accentuated and more conspicuous in the hybrid types, which gradually merge into the surrounding granite leaving only a series of parallel biotite-rich layers that mark the position of the original block of gneiss (Fig. 10). Large tongues of quartz and felspar also frequently develop in the larger blocks.

V. TECTONIC AND MAGMATIC HISTORIES.

It will not be possible to write either the tectonic or magmatic history of this area until further work has been done on the Ordovician metamorphic zones and upon the later granites in the Victorian sector; and also upon the relative ages of the various younger granites in the New South Wales part of the complex. A brief outline or introduction, however, will be attempted here and this will be more of the nature of a progress report on the tectonics.

At Cooma (Joplin, 1942, p. 194) petrological evidence suggested that compressional forces had been active before the injection of the magma, and that the schists had possibly been raised to the biotite-zone of regional metamorphism by such shearing stresses. As andalusite and cordierite are usually regarded as anti-stress minerals, it was suggested that stress declined at Cooma immediately after the injection of the magma and that the andalusite-zone was of the nature of a contact aureole. This explanation of the zoning seems to apply to the Albury–Jingellic region, and isoclinal folding and plicated structures suggest a strong compression. The lower grade rocks of the chlorite-zone, so well exposed north of Jingellic, do not usually show these structures and thus the metamorphic grade seems to be related to the degree of compression.

Fig. 10.

Angular fragments of cordierite-bearing gneiss rifted off and partly assimilated by Hawksview granite. Large fragments show patches and tongues of quartz and felspar that accentuate the original gneissic banding. At the top and at the extreme left of the figure, minute biotite-rich seams in the granite represent the last remains of almost totally resorbed fragments. These retain their original shape until complete resorption has taken place and the granite only contains a few clots of rather more basic composition.

Reference to Plate xv suggests that the knotted schists form zones about the two-mica gneisses, and in the neighbourhood of Jingellic, where no two-mica gneiss is exposed, it has been postulated that such a mass has been engulfed by a later granite, since by analogy elsewhere the arrangement of the knotted schists indicates its former presence.

It is suggested that the main injection of oligoclase-granite took place under conditions of declining stress; thus there was not so much development of injection-gneisses or of *lit-par-lit* structures as at Cooma; furthermore, permeation by magmatic fluids was not so marked. The andalusite and/or cordierite of the knotted schists, therefore, probably developed under high-grade thermal conditions where the pressure was mainly hydrostatic, and the granitization of the schists and the formation of the highly-contaminated gneisses took place under similar conditions.

Stress, however, was renewed later, and there was an injection of oligoclase-granite accompanied by pegmatite to form the abundant sills with which the granitized rocks and knotted schists are now threaded.

This region of Ordovician orogony possibly became a mobile belt again in Silurian time, when both the Mullanjandra gneiss and the porphyritic granite were injected. Finally, the same tract was probably the centre of orogony during Middle Devonian time and during the Kanimbla Epoch. As indicated by the work of Edwards and Easton, the same tectonic history applies in Victoria, thus suggesting the permanence of the mobile belts over several geological periods, and the successive injection of magmas into previously consolidated rocks of magmatic derivation.

VI. SUMMARY.

It has been shown that, as in the Cooma district, the Albury–Jingellic region consists largely of Ordovician schists in varying grades of metamorphism. A chlorite- and biotite-zone, a zone of knotted schists and a zone of granitized schists have been recognized, although zoning is not so perfect as at Cooma. This imperfection is due

to at least three factors: first, this region represents only the northern fringe of the large metamorphic complex of Victoria and the imperfection may be only local; secondly, a zone of sills is superimposed upon the higher grade zones and has been responsible for much greisenization; thirdly, later granites possibly of Silurian, Middle Devonian and Kanimbla ages have engulfed many of the schists, thus masking much of the metamorphic pattern, as well as superimposing their contact aureoles and producing new assemblages of metamorphic minerals.

VII. ACKNOWLEDGEMENTS.

In conclusion, the writer wishes to thank Dr. W. R. Browne for reading the manuscript of this paper and for his stimulating discussion and constructive criticism. She also gratefully acknowledges the help of Dr. J. A. Dulhunty, who kindly estimated the amount of carbon in five rocks, and of Miss Helen McRoberts, B.Sc., who measured the refractive index of the garnet in the cordierite-bearing gneiss. For assistance with field-work she wishes to thank Miss A. G. Culey, M.Sc., and Miss M. Breckenridge, B.Sc.

VIII. REFERENCES.

ALDERMAN, A. R., 1935.—Almandine from Botallack, Cornwall. *Min. Mag.*, 24 : 42.
————, 1936.—Eclogites from the Neighbourhood of Glenelg, Inverness-shire. *Quart. J. Geol. Soc. Lond.*, 92 : 501.
BAILEY, E. B., THOMAS, H. H., *et al.*, 1924.—Tertiary and Post-Tertiary Geology of Mull. *Mem. Geol. Surv. Scot.*, 23-25.
BARROW, G., 1893.—On an Intrusion of Muscovite-Biotite Gneiss in the South-Eastern High-lands of Scotland, and its Accompanying Metamorphism. *Quart. J. Geol. Soc. Lond.*, 49 : 343.
BOWEN, N. L., 1922.—The Behaviour of Inclusions in Igneous Magmas. *J. Geol.*, 30 : 513-570.
BROWNE, W. R., 1914.—The Geology of the Cooma District, N.S.W. Part i. *J. Roy. Soc. N.S.W.*, 48 : 172-222.
————, 1922.—Report of the Petrology of the Broken Hill Region, excluding the Great Lode and its Immediate Vicinity. *Mem. Geol. Surv. N.S.W.*, 8 App. 1, 30.
————, 1943.—The Geology of the Cooma District, N.S.W. Part ii. The Country between Bunyan and Collinton. *J. Roy. Soc. N.S.W.*, 77 : 165.
EDWARDS, A. B., and EASTON, J. G., 1937.—The Igneous Rocks of North-Eastern Benambra. *Proc. Roy. Soc. Vict.*, 50 : 69-96.
HARKER, A., 1932.—Metamorphism. London, 215.
HOWITT, A. W., 1884.—The Rocks of Noyang. *Proc. Roy. Soc. Vict.*, 20 : 18-70.
————, 1886.—The Sedimentary, Metamorphic and Igneous Rocks of Ensay. *Ibid.*, 22 : 63-127.
————, 1887.—Notes on the Area of Intrusive Rocks at Dargo. *Ibid.*, 23 : 127-164.
————, 1887-8.—Notes on Certain Metamorphic and Plutonic Rocks at Omeo. *Ibid.*, 24 : 100-131.
————, 1889.—Notes on the Metamorphic Rocks of the Omeo District, Gippsland. *Rep. Aust. Assoc. Adv. Sci.*, 1 : 206-222.
JOPLIN, G. A., 1942.—Petrological Studies in the Ordovician of New South Wales. i. The Cooma Complex. *Proc. Linn. Soc. N.S.W.*, 67 : 156-196.
————, 1943.—Id., ii. The Northern Extension of the Cooma Complex. *Ibid.*, 68 : 159-183.
————, 1944.—The Geology of the Albury District. *Ibid.*, 69 : 198-209.
————, 1945.—Petrological Studies in the Ordovician of New South Wales. iii. The Com-position and Origin of the Upper Ordovician Graptolite-bearing Slates. *Ibid.*, 70 : 158-172.
MACGREGOR, A. G., 1931.—Clouded Felspar and Thermal Metamorphism. *Min. Mag.*, 22 : 524-538.
NOCKOLDS, S. R., 1932.—The Contaminated Granite of Bibette Head, Alderney. *Geol. Mag. Lond.*, 69 : 433-452.
————, 1933.—Some Theoretical Aspects of Contamination in Acid Magmas. *J. Geol.*, 41 : 561-589.
READ, H. H., 1927.—The Igneous and Metamorphic History of Cromar, Deeside, Aberdeenshire. *Trans. Roy. Soc. Edinb.*, 55 : 317-353.
————, 1931a.—The Geology of Central Sutherland. *Mem. Geol. Surv. Scot.*, p. 145.
————, 1931b.—Corundum-spinel Xenoliths in Gabbro. *Geol. Mag. Lond.*, 68 : 450-452.
SEDERHOLM, J. J., 1928.—On Orbicular Granites, Spotted and Nodular Granites, etc., and on the Rapikivi Texture. *Bull. Comm. Geol. Finl.*, 83 : 91.
TATTAM, C. M., 1929.—The Metamorphic Rocks of North-Eastern Victoria. *Geol. Surv. Vict. Bull.*, 52 : 7-61.
TILLEY, C. E., 1925.—Metamorphic Zones in the Southern Highlands of Scotland. *Quart. J. Geol. Soc. Lond.*, 81 : 100-112.
————, 1940.—A Group of Gneisses (Sillimanitic and Cordieritic) from the Moraines at Cape Denison, Antarctica. *Aust. Antarctic Exped.*, 1911-14. Series A, 4 : 343.
WAHL, W., 1925.—Die Gesteine des Wiborger Rapakiwigebietes. *Fennia*, 45 (20) : 1-127.

THE DIPTERA OF THE TERRITORY OF NEW GUINEA. XIV.*

FAMILY TABANIDAE. PART II. PANGONIINAE, EXCEPT THÉ GENUS CHRYSOPS.

By H. OLDROYD, M.A., F.R.E.S.,
British Museum (Natural History), London.

(Communicated by Dr. G. A. M. Heydon.)

(Nine Text-figures.)

[Read 30th July, 1947.]

INTRODUCTION.

For several years before his death, the late Mr. Frank H. Taylor had been planning a revision of the Tabanidae of New Guinea and adjoining territories. For this purpose he had borrowed from the British Museum (Natural History) the collections made by Miss L. E. Cheesman, and, during 1945, Mr. Arthur Smith in London made for him a number of drawings of types and other noteworthy specimens. Unfortunately Mr. Taylor died in December, 1945, before he had completed more than the first paper of the series.

Professor Harvey Sutton very generously agreed to my suggestion that I should take over and complete Mr. Taylor's study, and sent to me the whole available material. The specimens comprise Miss Cheesman's collections from Papua, Japen Island, and the Cyclops Mts., a fine collection made by the Archbold Expedition of 1938–39 in Hollandia and the Lake Habbema–Mt. Wilhelmina region, and numerous specimens belonging to the Department of Public Health and Tropical Medicine, Sydney, many of them collected by Mr. Taylor himself in the Edie Creek area of NE. New Guinea—a total of 882 specimens. Miss Cheesman's collections are the property of the British Museum (Natural History), and the Archbold collections are held on loan from the Buitenzorg Museum, Java. Dr. Alan Stone and Dr. E. A. Chapin very kindly lent me 181 Tabanidae from the collections of the United States National Museum, Washington.

Along with the illustrations of 34 species made by Mr. Smith, I have received 13 figures drawn in Australia by Mr. E. H. Zeck, and a card-index of species prepared by Mr. Taylor. There is no manuscript nor notes, and the specimens have not been sorted. One or two random identifications have been made. It is evident that Mr. Taylor had barely completed the preliminary assembly of material and information. His paper on the genus *Chrysops*, published (posthumously) in these PROCEEDINGS in 1946, summarizes the New Guinea species, but records no new material. The genus is represented in the present material only by two females of *Chrysops albicincta* Wulp, one in the Archbold collection from Bernhard Camp, 50m., viii, 1938 (J. Olthof), and the other from Hollandia, July, 1945 (B. Malkin: Washington Coll.). Nothing in this or any subsequent paper of the series, therefore, represents any view held by Mr. Taylor unless the fact is expressly stated.

I am greatly indebted to Professor Harvey Sutton for his co-operation in sending me this material and for submitting the manuscript to the Linnean Society of New South Wales. Miss Cheesman very kindly gave me information about New Guinea and lent me her personal copy of the Archbold Reports. Mr. G. H. Hardy placed at my disposal a list of species he had compiled and sent me a summary of his views on the grouping of species of *Tabanus* in the Australasian fauna.

SCOPE OF PAPER.

This paper deals with the Pangoniinae, other than the genus *Chrysops*, in the collections before me. These divide into two groups, the hairy-eyed species which belong to the genus *Scaptia* Walker, and the bare-eyed species which were all formerly placed in *Silvius* Meigen. None of these is congeneric with the genotype of *Silvius*, and here they are referred to the genera *Pareucompsa* Enderlein and *Lilaea* Walker.

There is enough material to give some idea of distribution, and it is interesting that all the *Scaptia* were taken in mountainous areas above 2,000 ft., while the other two genera were taken in low-lying areas to north or south of the central mountain chain or on the coast. This is in agreement with the biological accounts of Fuller (1936) and Hill (1921).

The *Scaptia* individuals are very variable, and it is evident that there are many local forms and interlocking species. This might be expected in a genus living in mountainous habitats and liable to be divided into relatively isolated populations. It is difficult to judge from the examination of small collections of dried specimens which forms are good species and which are merely local races. Probably many more are still to be found in New Guinea.

The species of lowland habitat are much more uniform, and interesting chiefly in their generic relationships.

LOCALITIES.

Miss Cheesman gives accounts of her own collecting trips in her books, "The Two Roads of Papua" and "Land of the Red Bird", and in articles in the *Geographical Journal*. A full and most interesting illustrated account of the Archbold Expedition is given by Archbold, Rand and Brass (1942).

The following is the list of localities in the material I have seen:

Miss Cheesman's Collections.

		Lat. S.	Long. E.
PAPUA.	Mt. Tafa	08·38	147·07
	Mafulu	08·30	147·00
	Kokoda	08·52	147·40
	Mondo	08·34	147·07
	Yule I.	08·47	146·30
DUTCH NEW GUINEA.	Japen I.	01·40	136·20
	Cyclops Mts.	02·30	140·30
WEST NEW GUINEA.	Mt. Nomo.		

Archbold Expedition.

	Lat. S.	Long. E.
Hollandia	02·30	140·42
Araucaria Camp	03·30	139·11
Bernhard Camp	03·29	139·13
Habbema Lake	04·08	138·42
Iebele Camp	03·58	138·46
Moss Forest Camp	04·00	138·43
Top Camp	03·30	139·02
Rattan Camp	03·30	139·09
Mist Camp	03·30	139·05
Lower Mist Camp		

Other Collectors.

		Lat. S.	Long. E.
NE. NEW GUINEA.	Edie Creek	07·00	146·30
DUTCH NEW GUINEA.	Lorenz R.	05·27	138·00
	Regen I.	04·48	138·55
	Digul Mts.	05·07	140·35

Figure 1 shows the distribution of specimens in the present material.
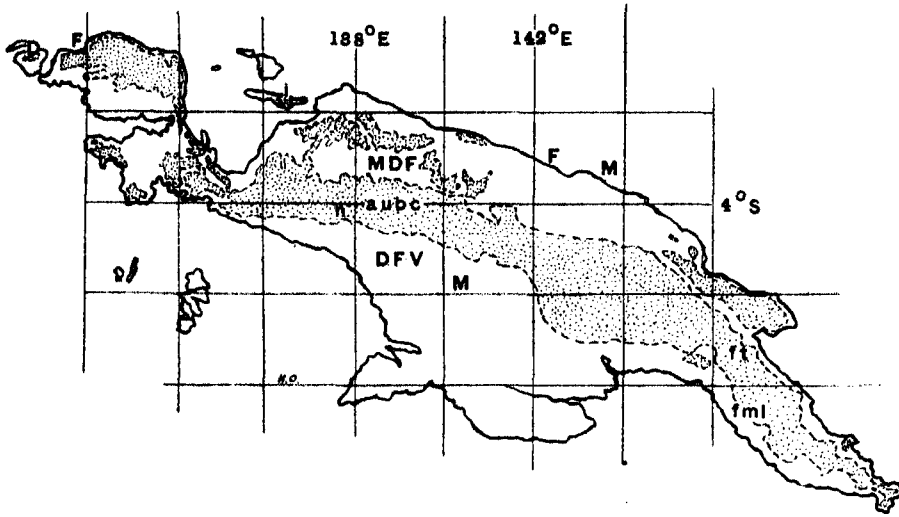
Fig. 1.—Localities of specimens mentioned in this paper.

Small letters, *Scaptia* spp.: a, *auripilosa*; b, *bernhardi*; c, *caliginosa*; f, *floccosa*; i, *insularis*; l, *leonina*; m, *mafulensis*; n, *novaeguineensis*; t, *taylori*; u, *unilineata*.

Capital letters: D, *Pareucompsa dimidiata*; F, *P. femoralis*; M, *Lilaea de meijerei*; V, *L. vittata*.

The shaded area represents the approximate extent of land above 2,000 ft.

KEY TO GENERA OF NEW GUINEA PANGONIINAE.

Hind tibiae with spurs: ocelli usually present.

1. Flagellum* of antenna with eight segments. Proboscis usually much longer than head. Eyes may be hairy 2

   Flagellum of antenna with four or five segments. Proboscis usually short, not greatly longer than head. Eyes bare 3

2. Eyes bare. Proboscis usually long or very long, held horizontally forward, face often conically produced. No ocelli .... *Nuceria* Walk.

   Eyes hairy. Proboscis not more than twice as long as height of head, held downwards at an angle of 45°. Ocelli present .... *Scaptia* Walk.

3. First and second antennal segments about equal in length. Wings with dark crossbands .... *Chrysops* Meig.

   Second antennal segment shorter than first. Wings clear or with dark crossbands 4

4. First antennal segment more than twice length of second. Frons very broad, with circular callus (Fig. 7) .... *Silvius* Meig.

   First antennal segment less than twice length of second. Frons 3-4 times as long as broad, callus club-shaped, reaching nearly to ocelli 5

5. Flagellum with four segments. Wings banded (Fig. 9) .... *Pareucompsa* End.

   Flagellum with five segments. Wings not banded .... *Lilaea* Walk.

Genus NUCERIA.

Nuceria Walker, 1850, *Ins. Saunds. Dipt.*, I, p. 7. Genotype: *Pangonius longirostris* Hardw., by designation of Coquillett, 1910.

Corizoneura Rondani, 1864, *Arch. zool. Modena*, 3, p. 85. Genotype: *Pangonia appendiculata* Macq. (*Tanyglossa aethiopica* Thunb.), by designation of Coquillett, 1910.

Stridorhina Enderlein, 1922, *Mitt. zool. Mus. Berl.*, 10, p. 336. Genotype: *Pangonius longirostris* Hardw., by original designation.

NOT: *Nuceria* Enderlein, 1922, p. 339 (= *Philoliche* Wied.).

   Corizoneura Enderlein, 1922, p. 337 (= *Ectenopsis* Macq.).

A genus recognized by the prominent, conical snout and elongate proboscis, which is often 2-3 times the length of the body. It is distinguished from *Pangonius* Latr. (*sensu stricto*) of the Palaearctic Region by the absence of ocelli, and from the African *Philoliche* Wd. by the usually open first posterior cell. This latter is not an infallible

---

* *Flagellum* here and throughout means the whole antenna beyond the first two segments (scape and pedicel).

K

guide and occasionally specimens occur with this cell closed in one or both wings. Perhaps this group of species is no more than subgenerically distinct from *Philoliche*, but it is convenient to separate them off from the large group of African species that have the first posterior cell decisively closed.

The length of the proboscis and degree of prominence of the face vary considerably between one species and another, and sometimes within one species. Bequaert (1930, p. 881) regards both these characters as purely adaptive and varying together. A number of genera have been recognized among those species with a less strikingly developed snout.

I have seen no specimens of *Nuceria* from New Guinea, though *N. amboinensis* Fabr. might be expected to occur there. Schuurmans Stekhoven (1926, p. 67) records this species also from Timor, though his specimens have not such obvious thoracic stripes as the descriptions of Fabricius and Wiedemann would indicate.

In the British Museum is a series from Bigot's collection of an undoubted *Nuceria*, which he labelled "*amboinensis* F.", and which has prominent thoracic stripes. The locality is given simply as "E. Indes", and in view of Bigot's somewhat high-handed treatment of existing locality-labels the localities of his specimens are never altogether reliable. There is always confusion between "E. Indes" and "E. India". This species seems to be closely allied to the Indian *N. rufa* Macq., and, indeed, two further specimens in the series are labelled "Bombay". Altogether I have not much confidence in this identification, but if it should be correct it would seem that *N. amboinensis* is an off-shoot of the Indo-Oriental fauna and may not reach New Guinea.

Pangonia neocaledonica Mégnin was regarded by Ricardo as a synonym of *leucopicta* Bigot, of which the type, from New Caledonia, is in the British Museum. We have also a series of a similar, but smaller, species, which seems to be those specimens referred to by Bigot (1878, *Ann. Soc. ent. Fr.*, (5) viii, Bull. cxlv, p. 139) in his augmented description of Mégnin's species. It seems as if two species are concerned here, but neither is a typical *Nuceria*, nor—since they lack ocelli—can they be referred to *Buplex*. In facial structure they seem most nearly to approach the African groups *Philoliche* and *Ommatiosteres*. The Washington material contains two females of *leucopicta* from Koumac, New Caledonia, 16.xi.45 (D. G. Hall). I have not seen either species from New Guinea.

Genus SCAPTIA.

Scaptia Walker, 1850, *Ins. Saunds. Dipt.*, I, p. 8. Genotype: *Pangonius auratus* Macq.

Melpia Walker, 1850, Ibid., I, p. 8. Genotype: *Pangonius fulvithorax* Wied.

Osca Walker, 1850, Ibid., I, p. 10. Genotype: *Pangonius depressus* Macq. (*Tabanus latus* Guér.)

Diatomineura Rondani, 1864, *Arch. zool. Modena*, 3, p. 84. Genotype: *Pangonius depressus* Macq.

Erephopsis Rondani, 1864, Ibid., 3, p. 85. Genotype: *Pangonius fulvithorax* Wied.

All the above genotypes designated by Coquillett, 1910.

The synonymy of this genus has been discussed by Ferguson (1926, pp. 294–299), who also suggested lines along which the genus might subsequently be divided.

Apart from the "Pangonie fuligineuse" of Boisduval, considered and rejected by Ferguson (1924, p. 257), three species of *Scaptia* have been recorded from New Guinea: *caliginosa* Walk., *novaeguineensis* Ric., and *albibarbis* S.S. In the British Museum, I have the type of the first and a paratype of the second, but I have not seen the third. Miss Cheesman, Archbold and Taylor all took specimens of this genus.

With the exception of *novaeguineensis*, the New Guinea species of *Scaptia* are of uniform appearance, and the differences between them are mainly small details of colour and pattern. The shape of the palpi, especially the relative extent of the bare area, is helpful in separating some species, but is subject to individual variation. I have not found any significant differences in the relative length of palpi and proboscis (cf., Ferguson, 1926).

The material I have studied can readily be divided into a number of units, but it is notable that each unit is made up of specimens from the same, or closely neighbouring, localities. It is likely, therefore, that some of these units will prove to be geographical races rather than distinct species. This is particularly true of the two species *floccosa* and *insularis*, which may be forms of *caliginosa* Walk. *S. taylori* is closely related, but since it occurs at Edie Creek with a normal specimen of *floccosa* it would seem to be a good species.
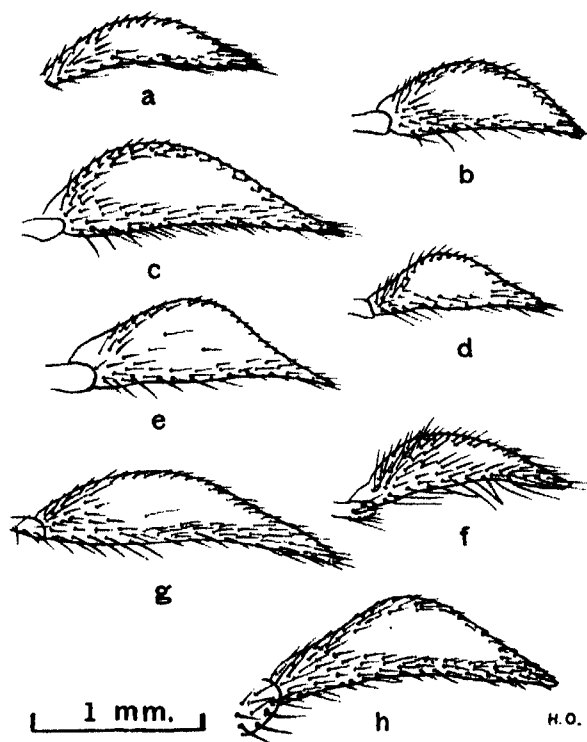
Fig. 2.—*Scaptia* spp., second segment of palp: a, *unilineata*; b, *mafulensis*; c, *insularis*; d, *leonina*; e, *caliginosa*; f, *auripilosa*; g, *floccosa*; h, *bernhardi*.

I have not recognized *albibarbis* S.S. From the description it seems to be close to my species *unilineata*, but differs in a number of details, the pubescence of the eyes, the pale hairs posteriorly on the scutum, black hypopleural bristles, and in the abdominal pattern.

In descriptions of the wing-pattern I have referred to the basal and apical bands. These are well shown in Mr. Zeck's figure of *floccosa* (Fig. 6).

KEY TO SPECIES OF SCAPTIA.

1. Thorax and abdomen with uniform covering of golden hairs 2
   Abdomen without golden hairs, except in median triangles, and perhaps laterally 4
2. Large yellow species (17 mm.). Hairs of eyes short, pale, relatively sparse
   novaeguineensis Ric.
   Small species (12 mm.). Hairs of eyes long, dark brown, dense 3
3. Frons and facial swelling grey in ground colour, with brown tomentum. Palpi with a small bare area (Fig. 2f), and with long yellow hairs below. Parafacials with mostly black hair .... *auripilosa*, n. sp.
   Frons and facial swelling reddish in ground colour, with brown tomentum. Palpi with bigger bare area (Fig. 2d), hairs short, black. Parafacials bare, no hairs between antennae and mouth-margin .... *leonina*, n. sp.
4. Palpi with small bare area (Fig. 2a). Frons and facial swelling grey in ground colour, with greyish tomentum. Abdomen distinctly paler and more translucent at sides, with

median black spot on second segment and median triangles of yellow hairs.   Other
abdominal hairs yellow on segmentations, black elsewhere .... *unilineata*, n. sp.
Palpi not as figured. Frons and facial swelling usually orange in ground colour   5
5. Larger species (15 mm.).   Meso- and sternopleura with varying amounts of dark brown
   or black hair, mixed with some yellow.   Wings with pattern indistinct and colour
   rusty .... *bernhardti*, n. sp.
   Smaller species (10-13 mm.).   Pleura with pale hairs only.   Wings usually with pattern
   clear-cut, and colour dark brown   6
6. Parafacials with conspicuous tuft of yellowish hairs.   Mesonotum with some yellow hairs
   before scutellum, which has black hairs.   Abdominal hairs black, pale yellow triangles
   and yellowish tufts on sides of segments 1, 2 and 6 .... ? sp.
   No conspicuous pale parafacial tuft   7
7. Wings with basal band and a slight tinting of foreborder, but with no trace of a brown
   cloud or band across apex of discal cell.   Small species with shining yellow-brown
   abdomen and yellow femora .... *mafulensis*, n. sp.
   Wings with either a distinct apical band or at least a cloud at apex of discal cell   8
8. Palpi broad, leaf-like (Fig. 4).   Wings with a distinct cloud at apex of discal cell
                                                                            taylori, n. sp.
   Palpi longer, blade-like, 4½ times as long as their greatest breadth.   Wings with apical
   band distinct   9
9. Eyes with pile short, pale, sparse .... *caliginosa* Walker
   Eyes with pile long, brown, thick   10
10. Abdomen with median triangles of yellow hair.   Mesonotum with fine golden hairs just
   before scutellum, pleural tufts not conspicuous in dorsal view .... *insularis*, n. sp.
   Abdomen without median triangles of yellow hairs.   Mesonotum without golden hairs.
   White pleural tufts very conspicuous in dorsal view .... *floccosa*, n. sp.

SCAPTIA NOVAEGUINEENSIS.

Erephopsis novaeguineensis Ricardo, 1913, *Nova Guinea*, ix, zool., 3, p. 404; Schuurmans
   Stekhoven, 1926, *Treubia*, vi, suppl., p. 64.

This species, of which the paratype is in the British Museum, is very distinct from
any other New Guinea species by its large size, yellow appearance, and pale wings.
It has been fully described by Ricardo and Schuurmans Stekhoven. Apparently no more
specimens have been recorded since the original description.

   Type Locality: Mt. Hellwig (Lorenz).

SCAPTIA AURIPILOSA, n. sp.

Lake Habbema, 10,000 ft., viii (Toxopeus).   Type ♀ and paratypes 1 ♀, 1 ♂.   Type in
   Buitenzorg Museum, Java.

One of the two species in the present collection in which the abdomen is covered
uniformly with short golden hairs. Distinguished by the shape of the palpi (Fig. 2f),
which have long yellow hairs, especially ventrally. The frons and face are blackish-
grey in ground colour, and cinereous in appearance.

   ♀. *Head.* Frons and face blackish-grey in ground colour, with brown tomentum.
Hairs black, except on parafacials where there are some yellow hairs. Beard white.
Eyes with pile long, somewhat sparse, dark brown. Antennae: first two segments
brownish, with brownish tomentum, mixed black and yellow hairs, third segment
bright orange. Palpi as figured (Fig. 2f). Proboscis 3½ times as long as palpi.

   Thorax. Dark brown, with cinereous dusting. Hairs on scutellum and side-margins
mostly orange, upright hairs on mesonotum black, recumbent hairs golden. Pleura
grey, with white hairs, the propleural and mesopleural tufts partly orange.

   Abdomen. Tergites uniformly chocolate-brown, with recumbent golden hairs, lateral
margins and last three tergites with a few long black hairs. Venter obscurely yellow,
with longer golden hairs.

   Legs. Orange, tarsi and anterior faces of femora somewhat darkened. Long hairs
mostly golden on femora, mostly black elsewhere.

   Wings. Yellowed on foreborder. Basal band faint, apical band absent. Tegulae
with black hairs and isolated golden ones. Subepaulets blackish.

   Length. Body 12 mm.; wing 12 mm.

   ♂. Similar, except that over the whole body black hairs are longer and more
numerous. Abdomen orange at sides basally, recumbent golden hairs tending to bunch
into indistinct median triangles.

SCAPTIA LEONINA, n. sp.

Papua, Mt. Tafa, 8,500 ft., iii, 1934 (Miss Cheesman). Type ♀ and paratypes 1 ♀, 1 ♂. Type in British Museum.

Similar to *auripilosa*, of which it might possibly prove to be a light form. The palpi, however, are different (Fig. 2d), parafacial hairs are absent, thorax and abdomen are more translucent in ground colour, and there are no black hairs on the thorax and very few isolated ones on the abdomen after the first segment.
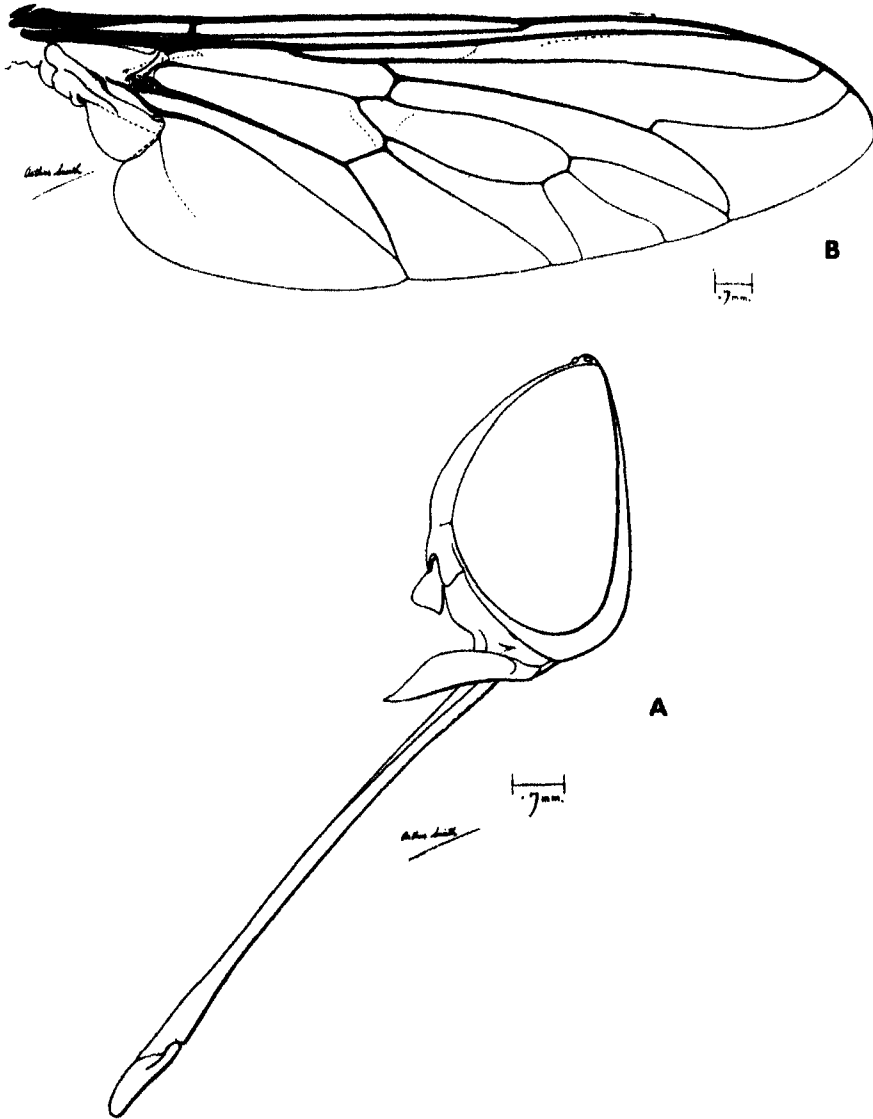

Fig. 3.—*Scaptia novaeguincensis* Ric.: A, head; B, wing. Both from paratype. (Antennae broken.)

♀. *Head.* Frons and face reddish-brown in ground colour, with thick brown tomentum and brown hair. Parafacials bare except for one or two isolated hairs in the lower angle. Beard white. Eyes with pile long, moderately thick, brown. Antennae: first two segments yellow, with yellow tomentum and mixed black and yellow hairs, third segment bright yellow, darker at tip.

Thorax. Yellowish-brown, translucent, with faint cinereous dusting. Hairs long and silky, fawn or reddish. Pleura greyish with pale yellow hairs.

Abdomen. Translucent yellow, obscurely blackish after second segment. First tergite and part of second with fine black hairs, rest of abdomen with golden or reddish hairs. Venter similar.

Legs. Yellow, including tarsi, with predominantly yellow hairs, coxae with long silky yellow hairs.

Wings. Yellowed on foreborder, with distinct basal band clouding base of discal cell, and a very small, indistinct spot at apex of discal cell. No distinct apical band. Tegulae with reddish hairs, subepaulets yellow or blackish.

Length. Body 11 mm.; wing 11 mm.

♂. Very similar, but with hairy parafacials and somewhat darker abdomen.

<div align="center">SCAPTIA UNILINEATA, n. sp.</div>

Dutch New Guinea, Iwaka R., 7.xi.1910 (Wollaston). Type ♀. Iebele Camp, 7,000 ft., 18.xi.1938, 1 ♀, 1 ♂. Moss Forest Camp, 8,000 ft., 24.x.38, 2 ♀♀ (Toxopeus). Bernhard Camp, 2,000 ft., 20.x.38 (Olthof), 1 ♀. Type in British Museum.

A species distinguished by the blackish frons, palpi with a relatively small bare area, and reddish abdomen with a distinct median black spot on the second segment.

♀. *Head.* Frons black in ground colour, with grey and brown tomentum and black hairs. Face reddish-brown, heavily tomented, hairs mostly black, some yellow. Parafacials with some pale hairs in type, bare in some paratypes. Beard white. Eyes with pile long, brown. Antennae: first two segments brown, with brown tomentum and mostly black hairs, third segment orange, scarcely darkened at tip. Palpi as figured (Fig. 2a). Proboscis 3–3½ times as long as palpi.

Abdomen. Translucent orange, with a conspicuous median black area on first and second tergites; later tergites may be obscurely blackish, especially in greasy specimens. Hairs mainly black, with silky yellow hairs in median triangles and on side-margins. Some black hairs in lateral tufts on segments 3-5. Venter orange, obscurely blackish, hairs mainly yellow.

Legs. Femora blackish, tibiae and tarsi orange, darkened at tips, hairs mixed black and yellow. Coxae with mainly black hairs.

Wings. Basal band distinct, apical band fainter, and the brown colour more pronounced along the veins. Apex of discal cell and base of radial fork distinctly clouded. Tegulae with black hairs, subepaulets blackish.

Length. Body 11 mm.; wing 12 mm.

♂. Similar, except that black hairs are longer and more numerous, especially on venter, and a few are present on mesopleuron. First two antennal segments black, contrasting sharply with orange flagellum.

<div align="center">SCAPTIA BERNHARDI, n. sp.</div>

Bernhard Camp, 2,500 ft., x.1938 (Olthof). Type ♀ and paratypes 1 ♀, 1 ♂. Type in Buitenzorg Museum, Java.

This species is distinguished from the other New Guinea species, except *novaeguineensis*, by its larger size and by the shape of the head, which in dorsal view is distinctly triangular, not smoothly rounded as in the other species. The wings are strongly yellowed all over, with a rusty appearance.

♀. *Head.* Frons and face reddish in ground colour, with brown tomentum, hairs dark brown or black, a few paler. Hairs of parafacials black. Eyes with pile short, rather light brown, moderately thick. Beard yellow or brownish. Antennae: first two segments reddish, with reddish tomentum and black hairs, third segment orange with darker tip. Palpi as figured (Fig. 2h). Proboscis four times as long as palpi.

Thorax. A dark reddish-brown, paler above wings and on hind margin of scutellum, pleura dark reddish-brown. Hairs on dorsum black, those on lateral callosities and on pleura mixed black and yellow. Black predominate in one female, yellow in the other,

but the presutural tuft, and those on mesopleuron, sternopleuron and coxae are mainly black in both specimens.

Abdomen. Tergites reddish-brown, with black hairs, no trace of median triangles. Venter similar, but with a few short yellow hairs on hind margin of some segments. Lateral tufts black.

Legs. Blackish-brown, with black hairs and bristles.

Wings. Distal band absent, proximal band faded to a yellow-brown. The whole wing, except for the middles of the discal and basal cells, is yellowed, giving it a rusty appearance to the naked eye. Tegulae with black hairs, subepaulets blackish.

Length. Body 15 mm.; wing 16 mm.

♂. Resembles the female except in the following details: eyes more rounded in dorsal view, with thick brown pile; frons blackish with silvery tomentum; face a darker brown in ground colour; abdominal hairs longer and more erect, all black.

SCAPTIA MAFULENSIS, n. sp.

Papua, Mt. Mafulu, 4,000 ft., xii.33 and i.34 (Miss Cheesman). Type ♀ and 3 paratype ♀♀.
Type in British Museum.

Distinguished from the *caliginosa* group of species by the sparser, paler pubescence of the eyes and the entire absence of the distal band of the wing. It is paler in general ground colour than those species.

♀. *Head.* Frons and face reddish-yellow in ground colour, with yellowish tomentum, especially at sides, hairs black with some yellow, especially on face and antennary segment (sub-callus). Hairs of parafacials mainly black. Beard whitish. Eyes with pile somewhat paler and sparser than in *caliginosa* group. Antennae: first two segments reddish-yellow, with yellow tomentum and hairs mainly black, one or two ventral ones yellow; third segment bright orange, slightly darkened at tip. Palpi as figured (Fig. 2b). Proboscis 3½ times as long as palpi.

Thorax. Reddish-brown with a thin, uniform tomentum. Dorsum with black hairs, a few paler ones on margins. Presutural tuft black, supra-alar black above, yellowish below, postalar mainly black. Pleura yellow or reddish-yellow in ground colour, with entirely white hairs.

Abdomen. Tergites shining translucent yellow, with black clothing hairs. Some trace of small yellow median triangles. Lateral margins with isolated pale hairs, but no distinct tufts. Venter similar, with yellowish hairs.

Legs. Pale yellow. Coxae with pale hairs above, some black hairs below. Femora dorsally with pale hairs, tibiae and tarsi ventrally with red bristles; otherwise hairs and bristles black.

Wings. Usual pattern much reduced. Yellow foreborder and basal brown band still present, but apical band entirely absent, leaving only a faint general tinting of the whole apex of the wing. Tegulae with black hairs anteriorly, golden hairs posteriorly, subepaulets pale, bare.

Length. Body 10 mm.; wing 11 mm.

SCAPTIA TAYLORI, n. sp.

N. New Guinea, Edie Creek, 6,550–7,000 ft. (Taylor). Type ♀ and 11 paratype ♀♀. Type in School of Public Health and Tropical Medicine, Sydney.

Smaller than the *caliginosa* group, the distal dark band of the wing less distinct, palpi broader.

♀. *Head.* Frons and face obscurely orange in ground colour, with thick brown tomentum and black hairs. Hairs of parafacials mingled black and yellowish. Beard yellowish-white. Eyes with pile long, thick and brown, somewhat paler ventrally. Antennae: first two segments reddish-yellow, with tomentum and black hairs, third segment reddish, slightly darkened towards tip. Palpi as figured (Fig. 4). Proboscis not more than 3 times as long as palpi.

Thorax. Reddish-brown, with grey tomentum and traces of a narrow central dark stripe, scutellum similar. Dorsum clothed with long, very fine black hairs, among

which are a few isolated yellowish hairs, but these are not obvious. Presutural tuft black, with some yellowish hairs; supra-alar and post-alar mainly whitish with some black hairs. Pleural tufts all yellowish-white.

Abdomen. Tergites shining reddish-brown with irregular black patches, especially towards tip, segmentations translucent yellowish. Clothing hairs black, with very small
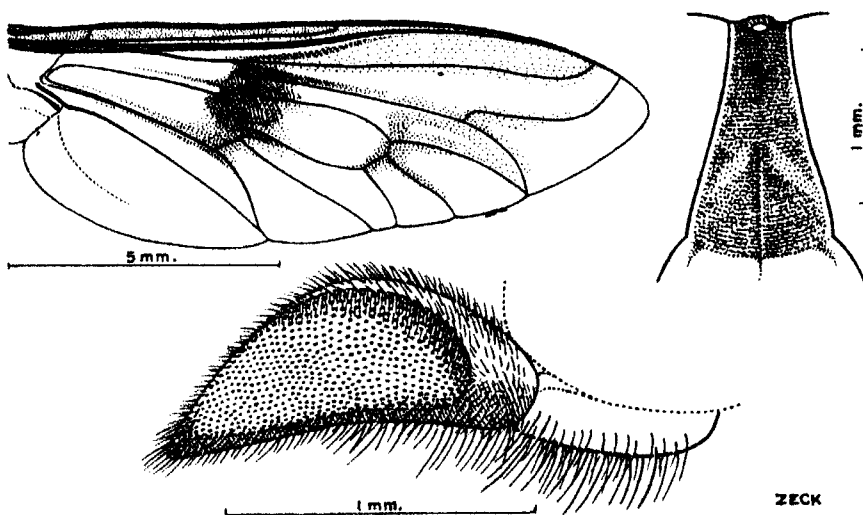
Fig. 4.—*Scaptia taylori*, n. sp.: wing, frons and palp.

median triangles of yellow hairs. Lateral margins without any thick tufts, but with a fringe of yellowish hairs. Venter similar in ground colour, with recumbent yellow hairs, black on sixth and seventh sternites.

Legs. Yellow or reddish-yellow. Coxae tomented, with mixed yellowish and black hairs. Femora with yellowish hairs above, otherwise hairs and bristles mostly black, long ventral bristles red.

Wings. Usual pattern somewhat reduced, so that the apical band is represented by a small, not very distinct, cloud at apex of distal cell (Fig. 4). Tegulae with black hairs anteriorly, golden hairs posteriorly; subepaulets bare, yellow, with golden sheen.

Length. Body 12 mm.; wing 13 mm.

<div align="center">SCAPTIA CALIGINOSA.</div>

Scaptia caliginosa Walker, 1865, *J. Proc. Linn. Soc. Lond.*, 8, p. 108.
Diatomineura caliginosa Ricardo, 1900, *Ann. Mag. Nat. Hist.*, (7) 5, p. 118; 1913, *Nova Guinea*, ix, zool., 3, p. 403.
Erephopsis caliginosa Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 62.

Schuurmans Stekhoven makes the odd mistake of quoting as type of this species a female collected by Wollaston in the Upper Utakwa Valley in March, 1912—forty-seven years after the original description! He states that he saw two females of this species in the British Museum, both collected by Wollaston. It seems that he did not see the real type specimen, which bears a label in Walker's handwriting "caliginosa n", and labels of later date reading "New Guinea" and "*Pangonia caliginosa* Walker, type". Neither Wollaston specimen appears to me to be conspecific with it. One I have made the type of my species *unilineata*; the other, which Schuurmans Stekhoven regarded as the type of *caliginosa*, has a conspicuous tuft of white hairs on the parafacials and is difficult to relate to any other specimens. It belongs near *caliginosa*, and may represent a variant of that species, but the specimen is in poor condition and I have to leave it undetermined. I do not understand why Schuurmans Stekhoven says the

first posterior cell is closed on the wing margin. This is not so in any of the three specimens referred to above.

The following description, taken from the specimen bearing Walker's label, differs from his description in two respects; the palpi are reddish, not black (pointed out by Ricardo, 1900), and there is no appendix to R_4. There is, however, a well-marked shadow which could easily be mistaken for a short appendix, and as Walker is known to have worked with very primitive optical equipment, I think this discrepancy should be disregarded.
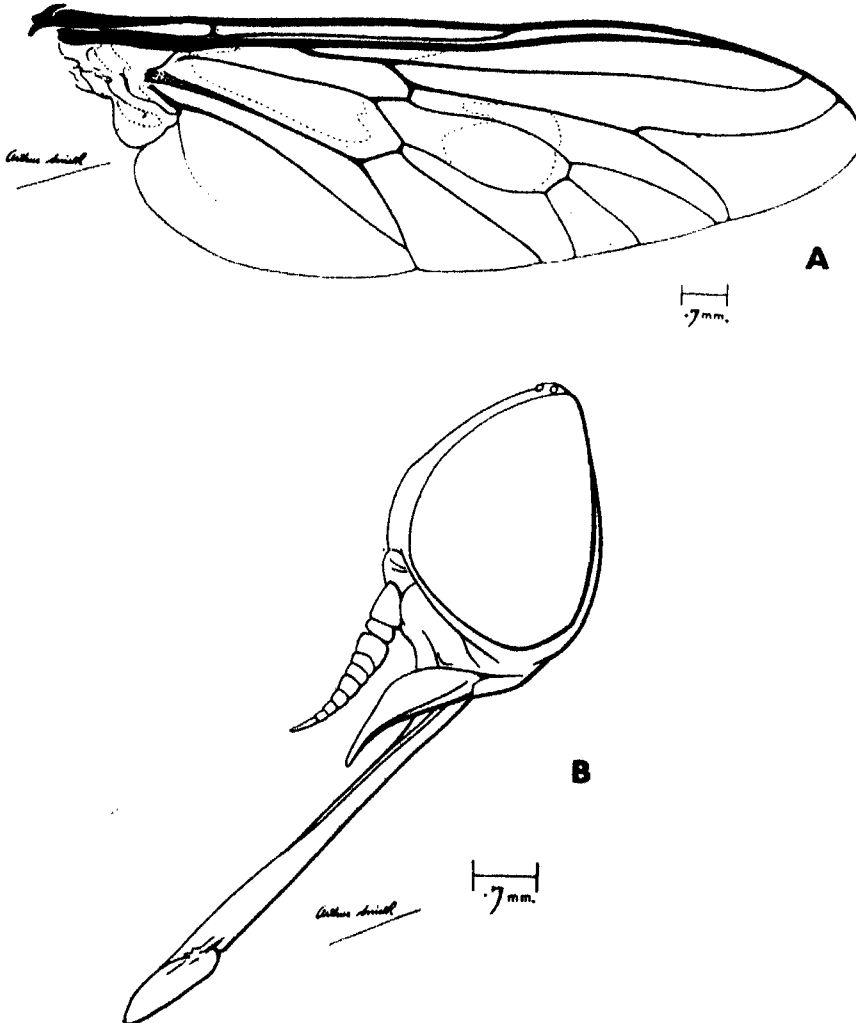
Fig. 5.—*Scaptia caliginosa* Walk.: A, wing; B, head. Both from type.

♀. *Head.* Frons very dark red in ground colour, with brown tomentum and black hairs. Subcallus and face more yellow-brown, latter with mostly black hairs. Parafacial hairs sparse, some pale. Beard snowy white. Eyes with pile sparse, pale and very short, except ventrally. I am not sure how far this can be attributed to the age of the specimen and to rubbing. Antennae: first two segments orange, with yellow tomentum and black hairs, flagellum bright orange, not darkened at tip. Palpi as figured (Fig. 2e), hairs short and black. Proboscis not more than three times length of palpi.

Thorax. Shining reddish-brown with grey tomentum and black hairs, except for a few pale ones in supra-alar and post-alar tufts. Presutural tuft black. Pleura orange, with grey tomentum and white hairs.

Abdomen. Denuded. Tergites shining mahogany-red, with black hairs and small median triangles of yellow hairs. Lateral tufts white. Venter similar, with mainly pale hairs.

Legs. Dark reddish-brown, obscurely blackish in parts, especially on anterior faces. Hairs, including those of coxae, mainly black.

Wings. With both basal and apical bands dark and well defined. R_4 without appendix. Tegulae with black hairs, subepaulets dark reddish. (Fig. 5 indicates only outlines of bands.)

Length. Body 13 mm.; wing 13 mm.

In the present collection the following series, though differing in some details from the type, appear to be conspecific. Bernhard Camp, 1,800–2,500 ft., 5.xi.38, 3 ♀♀; 2,100 ft., 10.xi.38, 1 ♀; 4,200 ft., 23.x.38, 2 ♀♀ (Olthof). Type in British Museum.

It is possible that the two following species are merely geographical forms of *caliginosa*. As represented in the present collection they are distinct units, but each series was collected in one area, *floccosa* in Papua, *insularis* in Japen I., and *caliginosa* in the central mountains of Dutch New Guinea. Until representatives from intermediate localities can be studied it is better to describe each form as a distinct species.

SCAPTIA FLOCCOSA, n. sp.

Papua, Mt. Tafa, 8,500 ft., ii.1934 (Miss Cheesman). Type ♀ and 3 paratype ♀♀; Kaindu, Edie Creek, 6,550–7,000 ft. (Taylor), 1 ♀. Type in British Museum.

A squarely-built species, abdomen rounded posteriorly, shining brown, with black hairs. Thorax with conspicuous white hairs laterally, eyes with dense, long brown pile, wings strongly marked.

♀. *Head.* Frons and face obscurely orange, with thick brown tomentum and black hairs. Parafacials with long black hair. Beard snowy white. Eyes with pile thick, long, dark brown. Antennae: first two segments yellow with black hairs, flagellum reddish, last three annuli blackish. Palpi as figured (Figs. 2g and 6), terminal point unusually long and narrow. Proboscis about 3½ times as long as palpi.

Thorax. Shining reddish brown, mesonotum with two indistinctly tomented grey stripes and clothed with sparse, fine, black hairs. Presutural tuft black, supra-alar and post-alar tufts very white, conspicuous in dorsal view. Pleura grey-tomented, hair-tufts pure white except for a few intermingled black hairs on the mesopleuron.
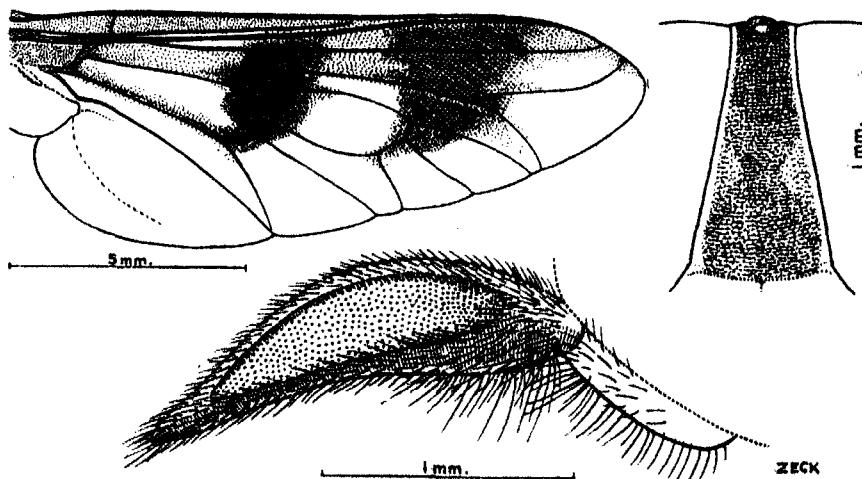
Fig. 6.—*Scaptia floccosa*, n. sp.: wing, frons and palp.

Abdomen. Shining reddish-brown, first segment mainly black, with a median extension of black colour on to second tergite, clothed with recumbent black hairs, without any pale median spots or triangles. Lateral tufts black except on segments 1, 2 and 6, where they are mainly white. Venter similar, somewhat darker towards tip, with black hairs, and with some white hairs on segments 1 and 2 and on the segmentations.

Legs. Yellow, slightly darker towards tarsi, with long black hairs. Coxae grey-tomented, with black or dark brown hairs.

Wings. With well-defined brown pattern (Fig. 6), tegulae with white tuft, sub-epaulets blackish.

Length. Body 13 mm.; wing 13 mm.

<div align="center">SCAPTIA INSULARIS, n. sp.</div>

Japen I., Camp 2, Mt. Elori, 2,000 ft., x.38. Paratypes 3 ♀♀; Japen I., Camp 1, Mt. Baduri, 1,000 ft., ix.38. Type ♀ and paratypes 5 ♀♀, 1 ♂; Papua, Mt. Tafa, 8,500 ft., ii.1934, 1 ♀ (Miss Cheesman). Type in British Museum.

Very similar to *floccosa*, from which it differs in having fine golden hairs on the mesonotum, especially just before the scutellum, and on the scutellar margin, and black hairs ventrally on the sternopleuron. White pleural tufts less conspicuous in dorsal view, black lateral tufts on segments 3, 4 and 5 of the abdomen weaker and less conspicuous, median triangles of yellowish hair can be traced on abdomen.

♀. *Head.* Frons and face obscurely orange in ground colour, with thick brown tomentum and black hairs. Parafacials with long, rather sparse black hair. Beard white. Eyes with pile thick, as long as first antennal segment, brown. Antennae: first two segments yellowish-brown with black hairs, flagellum reddish, not markedly darkened towards tip. Palpi as figured (Fig. 2c). Proboscis 3½ times as long as palpi.

Thorax. Reddish-brown, more heavily tomented than in *floccosa*, with traces of a dark median stripe anteriorly. Scutellum orange. Dorsum clothed with fine black hairs and intermingled, sparse, fine golden hairs, which are especially noticeable on the fore and hind margins of the scutellum. Presutural tuft black, with some yellowish hairs; supra-alar half black, half yellowish-white; post-alar white with a few fine golden hairs. These tufts are not conspicuous in dorsal view. Pleura reddish in ground colour, with grey tomentum, hairs white or yellowish, some black ventrally on sternopleuron.

Abdomen. Shining reddish-brown, first segment not markedly black, later segments blackish basally. Clothing hairs black; a small triangle of yellow hairs can be detected on all visible tergites. Lateral tufts less bushy than in *floccosa*, and mainly yellowish. Venter similar in ground colour, with rather sparse black hairs.

Legs. Yellow, slightly darker towards tarsi, with mixed black and yellow hairs. Coxae grey-tomented, white hairs dorsally, black hairs ventrally.

Wings. With well-defined pattern, both bands present. Tegulae with whitish tuft; subepaulets bare, clear yellow, in marked contrast to black bristles of base of costa.

Length. Body 12 mm.; wing 14 mm.

♂. Agrees with the female except in the following details: pale pubescence distinctly yellow; parafacials with yellow tuft; mesonotum with yellow hairs on anterior border, otherwise with only isolated golden hairs to be detected among black hairs of meso-notum and scutellum; abdominal tergites 3–6, blackish, with translucent yellow hind-margins. Black hairs more erect than in female, and median yellow triangles more conspicuous.

The female from Papua, Mt. Tafa, is provisionally assigned to this species. It differs from the Japen specimens in having blackish subepaulets, some pale hairs on the parafacials, and slightly differently shaped palpi. In some respects it is transitional between *insularis* and *floccosa*.

Genus SILVIUS.

Silvius Meigen, 1820, *Syst. Beschr.*, II, p. 27. Genotype: *Tabanus vituli* Fabr., monotypic.

The following species of Pangoniinae from New Guinea have been recorded in the genus *Silvius*: *dimidiatus* Wulp, 1868; *dimidiatus* subsp. *femoralis* Ricardo, 1913; *de meijerei*, *vittatus* Ricardo, 1913; *latistriatus*, *atriventer*, *atripes*, *variegatus*, ? *atratus* Schuurmans Stekhoven, 1926, and *flavicinctus* S. Stekhoven, 1932.

I have seen specimens of those species marked with an asterisk, none of which is a true *Silvius*. The genotype, a Palaearctic species, has a very broad, almost square frons, with a large, circular, shining callus, and the first antennal segment is more than twice as long as the second (Fig. 7). All the New Guinea species have a narrow, elongate
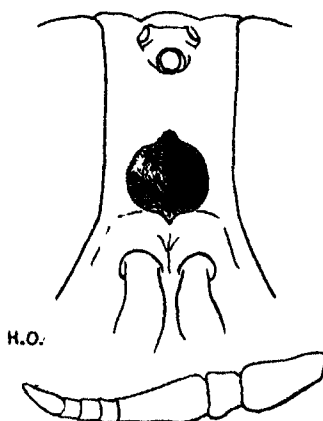
Fig. 7.—Frons and antenna of *Silvius vituli* Fabr., genotype of *Silvius*.

frons with a club-shaped callus which has a median extension reaching almost to the ocelli, and the first antennal segment is not much longer than the second (Fig. 8). All the specimens I have seen have the frons narrowest at the antennae, broadening towards the ocelli.

As long ago as 1880, Osten Sacken (*Ann. Mus. Civ. Genova*, 16, p. 419) stated that *Silvius dimidiatus* Wulp "is not a true *Silvius* because the antennae have a different shape and the eyes show trace of a broad crossband, while the known species of *Silvius* have greenish eyes, dotted with black". His specimen belonged to *femoralis* Ric., but that does not affect his argument. Ricardo (1913, p. 405) says the eyes of *vittatus* "appear to have one or more greenish crossbands, as in *S. dimidiatus*". I have not seen any clear trace of a crossband in any of my specimens, but Wulp mentions it and indicates it in his figure.

It seems clear, therefore, that the first four species on the list must be placed in a genus other than *Silvius*. I have not seen any of Schuurmans Stekhoven's species, but from the descriptions, *atriventer* and *flavicincta* seem to agree with this group in the structure of the frons. The others have no ocelli, and the frons, though elongate, is of variable shape.

Enderlein (1922, p. 344) erects a new genus *Pareucompsa* for *S. dimidiatus* Wulp because it has only four segments in the flagellum of the antennae (i.e., a total of six antennal segments)—one fewer than in true *Silvius*. This applies to *femoralis* also, but not to the other New Guinea species. Wulp and Schuurmans Stekhoven each figure five flagellar segments in *dimidiatus*, but they are wrong. Every specimen I have seen has only four, and an antenna cleared and mounted in balsam shows that there are four clearly-defined segments.

Since *dimidiatus* and *femoralis* have such a distinct facies, with *Chrysops*-like wings (Fig. 9), and thorax and abdomen strongly patterned, it is convenient to divide them off from the rest in this way. *Pseudopangonia* Ricardo, which also has four

flagellar segments, is a large, yellow, *Coenomyia*-like form; moreover, the flagellum is of altogether different construction, awl-like, with a broad basal segment and three longer, cylindrical ones. *Silviochrysops* Szilady, from Formosa, is rather inadequately described. The *Chrysops*-like wing-pattern seems to resemble that of *dimidiatus*, but the frons is described as squarish and the callus oval. There is no mention of the number of flagellar segments.

The two other New Guinea species I have seen—*de meijerei* Ric. and *vittatus* Ric.—although apparently closely related to *Pareucompsa* by the structure of frons and first antennal segment, yet can clearly be divided off by their five-segmented flagellum and their general appearance, with clear wings and a dull body-colour. They agree, in fact, with those Australian species hitherto included in the genus *Silvius*. As pointed out by Ferguson (1926, p. 301), these species fall into several groups, but as I have not made a close study of them I am not prepared to suggest any further subdivision. It is clear, however, that they do not belong to *Silvius*, and that some other name must be found for them.

The name *Lilaea* Walker is available and will be discussed below.

Genus PAREUCOMPSA.

Pareucompsa Enderlein, 1922, *Mitt. zool. Mus. Berl.*, 10 (2), p. 344; 1925, Ibid., 11 (2), p. 320. Genotype: *Silvius dimidiatus* Wulp, by original designation.

Distinguished from *Silvius* Meigen by the elongate frons and frontal callus, the shorter first antennal segment (Fig. 8A), and the reduction of the flagellar segments of the antenna to four. The two known species are distinctive in appearance, with a *Chrysops*-like wing-pattern, and thorax and abdomen divided into a light anterior half and a dark posterior half.

KEY TO SPECIES.

Femora blackish, concolorous with tibiae and tarsi. Second abdominal segment with a clear-cut transverse dark brown band, following segments more or less distinctly banded
.... *dimidiata* Wulp
Femora orange, contrasting with tibiae and tarsi, which are darker. Second abdominal segment without a transverse band, following segments obscurely darkened, but not distinctly banded .... *femoralis* Ric.

PAREUCOMPSA DIMIDIATA.

Silvius dimidiatus Wulp, 1868, *Tijdschr. v. Ent.*, xi, p. 6; Ricardo, 1901, *Ann. Mag. nat. Hist.*, (7) viii, p. 296; 1913, *Nova Guinea*, ix, zool., 3, p. 404; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 56.

This very distinct species is figured in colour by van der Wulp, and is easily separated from the following species by the characters given in the key. In both species the mesonotum is yellow-green before the suture and chocolate-brown behind it.
Length. Body 12 mm.; wing 10 mm.

Wulp described this species originally from Salawati I., and Ricardo records it from Regen I., Bivak I. (one of Lorenz's localities, presumably in the same general area), and Digul. In the present collection is a series of 29 females, all from Bernhard Camp, 150 ft., 4.viii–15.x.38 (Olthof)—i.e., in the river valley, close to the oxbow lake on which this camp was founded (Archbold *et al.*, 1942, p. 231). Two of Ricardo's specimens are in the British Museum, and there is one from Bigot's collection labelled simply "New Guinea". Type in Rijks Museum of Natural History, Leyden.

PAREUCOMPSA FEMORALIS.

Silvius dimidiatus Osten-Sacken, 1880, *Ann. Mus. Civ. Genova*, xvi, p. 478, nec Wulp.
Silvius dimidiatus subsp. *femoralis* Ricardo, 1913, *Nova Guinea*, ix, zool., 3, p. 405; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 57.

This species is distinguished from *dimidiatus* by the characters given in the key above. On the average it is slightly smaller.
Length. Body 11 mm.; wing 10 mm.

Ricardo described this as a subspecies of *dimidiatus*, presumably doubting whether the colour differences existing were sufficiently great to justify erecting a new species. These differences are very constant in all the spcimens I have seen. The two cannot be geographical races, since they occur together. Doré I., Osten-Sacken's locality, is quite near Salawati I., the type-locality of *dimidiatus;* both forms occur on Regen I.; and the Archbold Expedition took both together at Bernhard Camp. It is possible that this may be a dimorphic species, with two genetically distinct forms occurring roughly in the proportion of three to one, but there is no direct evidence for this. Until the two forms can be studied in the field it is better to regard them as distinct species.
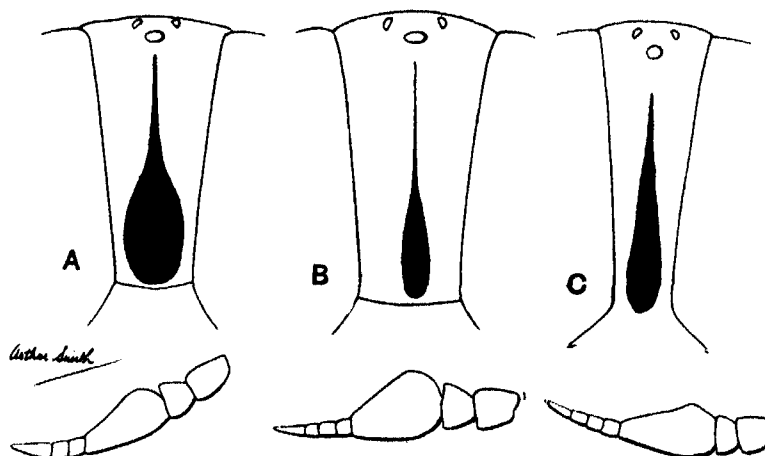
Fig. 8.—Frons and antenna of: A, *Pareucompsa dimidiata* Wulp; B, *Lilaea vittata* Ric.; C, *L. de meijerei* Ric.

Described from Regen I., Osten-Sacken's specimen, recorded as *dimidiatus*, was from Doré I. In the present collection 10 ♀♀ from Bernhard Camp, 150 ft., 4.viii–15.x.38 (Olthof): 1 ♀ Wewak (C. M. Deland). One of Ricardo's paratypes is in the British Museum. Type in Rijks Museum of Natural History, Leyden.

Genus LILAEA.

Lilaea Walker, 1850, *Ins. Saunds Dipt.*, I, p. 11; Surcouf, 1921, in Wytsman, *Genera Insect.*, 175, p. 561; Ferguson, 1924, *Bull. ent. Res.*, xiv, p. 254; 1926, Ibid., xvi, pp. 294, 302, 304. Genotype: *Pangonia lurida* Walker, by designation of Coquillett, 1910.

Distinguished from *Silvius* Meig. by the elongate frons and frontal callus, and the shorter first antennal segment (Figs. 8B, C), and from *Pareucompsa* End. by having five flagellar segments (total antennal segments seven). The New Guinea species are clear-winged, yellow to blackish-brown in colour, sometimes with abdominal markings like those of *Tabanus*.

There has been much confusion about this genus. Walker included two species, *roei* King and *lurida* Walk., and stated in his generic description: "stump of the tip cross-vein about twice the length of the shorter side of the angle from which it springs". Coquillett (1910) selected *lurida* as genotype. Enderlein (1922, p. 341; 1925, p. 297) erroneously selected *roei* as type, thus making the genus a synonym of *Scaptia*. According to his description and key, *Lilaea* had no appendix to R_4. Ferguson (1924, 1926) was puzzled by the discrepancy between Enderlein's description and Walker's, but omitted to notice that specimens of *lurida* identified by himself (now in the British Museum) also had no appendix to R_4. He sank *Lilaea* as a synonym of *Silvius*.

In the British Museum are the type specimen of *lurida* (Port Stephen, New Holland) and the second specimen from Swan River (Richardson). These are conspecific with modern specimens determined by Ferguson, and none of them has an

appendix to R$_4$. We therefore have the odd position of a genotype correctly selected from among the included species, and correctly identified from its type specimen, but which does not agree with the original generic description.
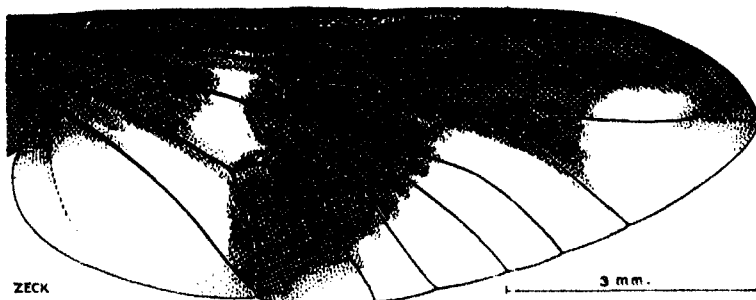
Fig. 9.—*Parcucompsa dimidiata* Wulp: wing.

In this instance, when the identity of the species is not in doubt, and we need a new name for the genus, I think we may disregard Walker's statement and resurrect the genus *Lilaea*. So far as I can see, it will include most of the Australian species hitherto placed in *Silvius*. I have not seen a true *Silvius* from Australia.

Ricardo (1900, *Ann. Mag. nat. Hist.*, (7) v, p. 121) says: "The *Pangonia lurida*, ♀, Walker is not a *Pangonia* at all; it belongs to the Tabaninae." This statement has contributed to the confusion about this species, and so far as I can see, it is without foundation. The type of *lurida* has lost both its hind legs, but the paratype has distinct spurs, and both specimens have ocelli.

LILAEA DE MEIJEREI.

Silvius de meijerei Ricardo, 1913, *Nova Guinea*, ix, zool., 3, p. 405.
Silvius de Meyeri Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 52.

A small species, of rather nondescript appearance. Thorax grey-brown, with a greenish tinge in certain lights. Abdomen yellow-brown basally, black-brown apically, with yellow segmentations, each fringed with yellow hairs. Frons broadened towards vertex, with elongate, club-shaped callus almost reaching ocelli.

Length. Body 10 mm.; wing 9 mm.

Distinguished from *vittatus* Ric. by the absence of the broad median stripe on the abdomen, and from the species described by Schuurmans Stekhoven by the shape of the frons.

Described from Rivierkamp (Lorenz) and the Digul River. In the present collection: Bernhard Camp, 150 ft., 7.viii.38–15.x.38 (Olthof), 23 ♀♀; Bernhard Camp, 300 ft., 10.iv.39 (Toxopeus), 2 ♀♀; Angoram (no date) (S. H. Christian), 6 ♀♀; N. New Guinea Exped., 1926, Motorbivak, vi (v. Leeuwen), 4 ♀♀. Type in Rijks Museum of Natural History, Leyden.

The two females taken in April by Dr. Toxopeus at a slightly greater altitude than the others can be correlated with the interesting account in Archbold *et al.* (1942, pp. 233 et seq.) of the wet season flooding of the Meervlakte and the change in conditions around Bernhard Camp.

LILAEA VITTATA.

Silvius vittatus Ricardo, 1913, *Nova Guinea*, ix, zool., 3, p. 405; Schuurmans Stekhoven, 1926, *Treubia*, vi, suppl., p. 49.

A clear-winged species, distinguished by the pale median stripe of the abdomen formed by a broad equilateral triangle on each segment, occupying about one-third of the width of the abdomen.

Length. Body 11 mm.; wing 10 mm.

Known to me only from the two paratypes collected by Lorenz and deposited in the British Museum, this species is not represented in the present collection. Type in Rijks Museum of Natural History, Leyden.

REFERENCES.

ARCHBOLD, R., RAND, A. L., and BRASS, L. J., 1942.—Summary of the 1938-39 New Guinea Expedition. *Bull. Amer. Mus. Nat. Hist.*, 79 : 197-288.

BEQUAERT, J., 1930.—Entomology : Tabanidae, in STRONG, *Rep. Harvard-African Exped. African Reps. Liberia, Belgian Congo* : 858-971.

CHEESMAN, L. E., 1935.—The Two Roads of Papua. Jarrolds, London.

————, 1938.—The Cyclops Mountains of Dutch New Guinea. *Geogr. J. Lond.*, (5) 91 (1) : 21-30.

————, 1940.—Two Unexplored Islands of Dutch New Guinea (Waigeu, Japen). Ibid., (5) 95 (3) : 208-217.

COQUILLETT, D. W., 1910.—The Type-Species of the North American Genera of Diptera. *Proc. U.S. Nat. Mus.*, 37 : 499-647.

ENDERLEIN, G., 1922.—Ein neues Tabanidensystem. *Mitt. zool. Mus. Berl.*, 10 (2) : 333-351.

————, 1925.—Studien über blutsaugenden Insekten. 1. Grundlagen eines neues System der Tabaniden. Ibid., 11 (2) : 255-409.

FERGUSON, E. W., 1924.—Notes on the Nomenclature of Australian Tabanidae, subfamily Pangoniinae. *Bull. ent. Res.*, 14 : 251-263.

————, 1926.—Additional Notes on the Nomenclature of Australian Tabanidae. Ibid., 16 : 293-306.

FULLER, M., 1936.—Biology of *Scaptia auriflua* Don. PROC. LINN. SOC. N.S.W., 61 : 1-9.

HILL, G. F., 1921.—The Bionomics of *Tabanus aprepes* and other Australian Tabanidae. *Bull. ent. Res.*, 12 : 41-62.

RICARDO, G., 1913.—Tabanidae of New Guinea. *Nova Guinea*, ix, Zool., 3 : 387-406.

SCHUURMANS STEKHOVEN, J. H., jnr., 1926.—The Tabanids of the Dutch East Indian Archipelago. *Treubia*, vi, Suppl. : 1-551.

————, 1932.—Résultats scientifiques du Voyage aux Indes Orientales Neerlandaises . . . Tabanidae. *Mem. Mus. Hist. nat. Belg.*, 4 (7) : 11-16.

TAYLOR, F. H., 1946.—The Diptera of the Territory of New Guinea. xiii. Family Tabanidae. Part i. The Genus *Chrysops*. PROC. LINN. SOC. N.S.W., 70 (for 1945) : 328-332.

TOXOPEUS, L. J., 1939.—Entomologische Notities uit Nieuw-guinea. *Ent. Meded. Ned.-Ind. Buitenzorg.*, 5 : 11-17 ; 24-37 ; 59-71 et seq.

WALKER, F., 1850.—Insecta Saundersiana, Diptera I.

REVISION OF AUSTRALIAN LEPIDOPTERA. OECOPHORIDAE. XIV.*

By A. Jefferis Turner, M.D., F.R.E.S.

[Read 28th May, 1947.]

This Part contains a number of genera, in which the male antennae have extremely minute ciliations or none. They appear to form a natural group, the Depressadiades of Meyrick, although this antennal distinction is not absolute. A remarkable form of pupa "naked, angular, and seated erect on a truncate tail, imitating a leaf" (Meyrick) is a structural character found in many genera, *Eutorna, Eupselia, Scorpiopsis, Peritorneuta, Tonica, Cryptolechia,* and others, which differ greatly in their imaginal state.

This revision commenced in 1932, and since then many new species have accumulated. These will be dealt with in the next Part.

Key to Genera.

L

174. Gen. ANCISTRONEURA, n.g. (ἀγκιστρονευρος, with hooked vein.)

Palpi long, ascending, recurved; second joint reaching base of antennae; terminal joint as long as second, slender, acute. Antennae longer than forewings; with strong pecten; in male simple. Forewings narrow; 7 and 8 stalked, 7 to costa. Hindwings lanceolate; 5 absent. Type, *A. thaumasia*.

2149. ANCISTRONEURA THAUMASIA, n. sp. (θαυμασιος, wonderful.)

♂, ♀. 20–22 mm. Head dark fuscous; face white. Palpi in female expanded, and second joint in male slender, smooth, but rough towards apex, fuscous, inner surface whitish. Antennae white with fuscous annulations, towards base rosy posteriorly. Thorax fuscous. Abdomen whitish. Legs fuscous; posterior pair whitish. Forewings narrow, elongate, costa straight to three-fifths, thence arched, apex acute, falcate, termen extremely oblique; grey; a slender subcostal line from base to three-fourths, whitish faintly rosy-tinged; a similar median line from one-half to beneath apex; a third line strongly curved from three-fourths dorsum to midtermen; a whitish costal line from three-fourths to apex; cilia grey, on apex fuscous, on costa whitish. Hindwings narrowly lanceolate; pale grey; cilia pale grey.

Queensland: Macpherson Rge. (3,000 ft.) in December. New South Wales: Sydney in March (G. M. Goldfinch).

2150. ANCISTRONEURA AMMOPHARA, n. sp. (αγκιστροτος, sandy-cloaked.)

♂. 18 mm. Head whitish-ochreous. Palpi with second joint thickened and rough anteriorly; fuscous. Antennae ochreous-whitish with blackish annulations. Thorax fuscous. Abdomen pale ochreous; tuft fuscous. Legs ochreous. Forewings narrow, costa straight to near apex, apex and termen broadly rounded; brownish-ochreous; a semilunar brown patch containing a central white spot, extending on costa to middle, and reaching half across wing; cilia whitish-ochreous. Hindwings grey; cilia whitish-ochreous.

North Queensland: Kuranda (F. P. Dodd); one specimen.

175. Gen. IDIOCHROA, n.g. (ἰδιοχρωος, peculiarly coloured.)

Palpi ascending, recurved; second joint not reaching base of antennae, smooth, slender; terminal joint smooth, slender, acute. Antennae as long as forewings; with pecten; in male minutely ciliated. Posterior tibiae hairy on dorsum. Forewings with 7 and 8 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal.

2151. IDIOCHROA ANTHINA, n. sp. (ἀνθινος, like a flower.)

♂. 12–14 mm. Head and thorax white, sometimes tinged with yellow. Palpi fuscous. Antennae 1; pale grey. Abdomen pale grey; tuft whitish. Legs whitish; anterior pair pale grey. Forewings narrow, posteriorly dilated, costa moderately arched, apex obtuse, termen straight, oblique; yellow, tinged with reddish towards costa; a rather broad oblique fuscous line from mid-dorsum, curved outwards above to two-thirds costa; a broad reddish-fuscous terminal line; cilia yellow. Hindwings and cilia whitish. In its colouring it resembles the genus *Crocanthes*.

Queensland: Nambour in November; Brisbane; Mt. Tamborine in November; four specimens.

176. Gen. PHOLEUTIS Meyr.

Exot. Micro., i, p. 307.

Palpi smooth, slender, ascending, recurved; second joint not reaching base of antennae; terminal joint shorter than second, acute. Antennae without pecten; in male simple. Forewings with 7 and 8 coincident. Hindwings lanceolate; neuration normal. Type, *P. neolecta* Meyr.

2152. PHOLEUTIS HOLOXYTHA Meyr., *Trans. Roy. Soc. S. Aust.*, 1906, p. 50. = *suffusca* Turn., *Proc. Roy. Soc. Qd.*, 1919, p. 128. (Nambour to Beaconsfield, Macpherson Rge., Ebor, Mt. Wilson.)

2153. PHOLEUTIS NEOLECTA Meyr., *Exot. Micro.*, i, p. 307. = *analcis* Turn., *Proc. Roy. Soc. Qd.*, 1919, p. 128. (Cairns, Nambour to Macpherson Rge.)

2154. PHOLEUTIS APREPTA, n. sp. (ἀπρεπτος, undistinguished.)

♂, ♀. 10–11 mm. Head and thorax fuscous. Palpi pale fuscous. Antennae fuscous. Abdomen fuscous; apices of segments on dorsum sometimes reddish. Legs pale fuscous; middle tibiae whitish. Forewings narrow, slightly dilated posteriorly, costa straight, apex rounded, termen obliquely rounded; fuscous, sprinkled with dark fuscous; cilia fuscous. Hindwings and cilia grey. The middle tibiae are whitish, not white as in *P. holoxytha.*

Queensland: Macpherson Rge. in November; three specimens.

2155. PHOLEUTIS LEUCOPREPTA, n. sp. (λευκοπρεπτος, decorated with white.)

♂. 12 mm. Head dark fuscous; face brassy-whitish. Palpi ochreous-whitish; apex of terminal joint fuscous. Antennae dark fuscous, apical eighth white, sharply defined. Thorax whitish. Abdomen fuscous. Legs fuscous. Forewings narrow but somewhat dilated posteriorly, costa slightly arched, apex rounded, termen very obliquely rounded; fuscous; a short inwardly oblique mark from costa before middle; a large circular blackish spot above dorsum beyond middle; followed by ill-defined subcostal and subdorsal dots; a white subcostal spot beneath three-fourths costa; cilia fuscous. Hindwings and cilia grey.

Queensland: Macpherson Rge. (4,000 ft.) in December; one specimen.

2156. PHOLEUTIS ACROPREPTA, n. sp. (ἀκροπρεπτος, with decorated tips.)

♂. 10–12 mm. Head and thorax fuscous; face and palpi whitish-ochreous. Antennae fuscous; apical fifth white, sharply defined. Abdomen fuscous. Legs fuscous; anterior and middle tibiae and tarsi with whitish-ochreous rings. Forewings narrow, apex rounded, termen very obliquely rounded; fuscous with slight purple gloss; a whitish-ochreous longitudinal mark in middle of disc at three-fifths; a series of minute whitish-ochreous dots very near termen; cilia fuscous. Hindwings and cilia dark grey.

Queensland: Macpherson Rge. (3,500 ft.) in December and January; four specimens.

177. Gen. LEPTOCOPA Meyr.

Exot. Micro., ii, p. 220.

Palpi ascending, recurved, long, slender, smooth; terminal joint long. Antennae with pecten; in male simple, serrulate. Forewings with 7 and 8 stalked, 7 to termen. Hindwings lanceolate; 3 and 4 coincident. Monotypical. I do not know this genus.

2157. †LEPTOCOPA NOTOPLECTA Meyr., *Exot. Micro.*, ii, p. 221. (Cairns.)

178. Gen. MELEONOMA Meyr.

Exot. Micro., i, p. 255.

Palpi ascending, recurved; second joint reaching base of antennae, slightly thickened with appressed scales; terminal joint shorter than second, slender, acute. Antennae without pecten; in male simple. Forewings with 7 and 8 stalked, 7 to costa. Hindwings lanceolate; neuration normal. Type, *M. stomota* Meyr. from India. There are five species from Borneo, Ceylon and India.

2158. †MELEONOMA PSAMMOTA Meyr., *Exot. Micro.*, i, p. 304. (St. Helens.)

2159. MELEONOMA CAPNODYTA Meyr., *Trans. Roy. Soc. S. Aust.*, 1906, p. 35. (Atherton, Townsville, Duaringa, Brisbane.)

2160. †MELEONOMA BASANISTA Meyr., *Exot. Micro.*, ii, p. 513. (Melbourne.)

179. Gen. SCHALIDEUTIS Meyr.

J. Bombay Nat. Hist. Soc., xvii, 1906, p. 409.

Palpi short, slender, ascending, recurved; second joint not reaching base of antennae; terminal joint shorter than second, acute. Antennae without pecten; ciliations in male short (one-half). Forewings with 7 and 8 stalked, 7 to costa. Hindwings lanceolate; 5 absent. Type, *C. escharias* Meyr. from Ceylon.

2161. SCHALIDEUTIS COCYTIAS Meyr., *Exot. Micro.,* 1, p. 307. (Brisbane, Stanthorpe, Gisborne.)

180. Gen. LEUROBELA, n.g. (λευροβελδς, with smooth weapons (palpi).)

Palpi smooth, slender, ascending, recurved; second joint not reaching base of antennae; terminal joint two-thirds to 1, acute. Forewings with 7 and 8 stalked; 7 to costa. Hindwings lanceolate; neuration normal. Type, *L. holophaea* Turn.

2162. LEUROBELA HOLOPHAEA Turn. *Proc. Roy. Soc. Qd.,* 1919, p. 127. (Ebor.)

2163. LEUROBELA CLASTOMITA, n. sp. (κλαστομιτος, with broken thread.)

♀. 15 mm. Head, thorax and palpi whitish. Antennae whitish with fuscous annulations. Abdomen grey. Legs whitish. Forewings narrow, costa slightly arched, apex rounded, termen very oblique; whitish with a few dark fuscous scales; markings dark fuscous; first discal at two-fifths, united by an interrupted line through second discal at two-thirds, and prolonged to apex, plical before first discal; an interrupted terminal line; cilia whitish with a few fuscous points. Hindwings and cilia pale grey.

Queensland: Macpherson Rge. (2,500 ft.) in November; one specimen.

2164. LEUROBELA PUNCTA, n. sp. (*punctus,* dotted.)

♂. 12 mm. Head and thorax white. Palpi fuscous; terminal joint and apex, of second whitish. Antennae grey. Abdomen fuscous. Legs fuscous; posterior pair whitish. Forewings narrow, costa slightly arched, apex pointed, termen very oblique; white; stigmata minute, blackish, approximated, first discal at one-fourth, plical beyond it, second discal at one-half; a dot above tornus; cilia white. Hindwings and cilia pale grey.

North Queensland: Stannary Hills, Atherton Tableland (Dr. T. Bancroft); two specimens.

181. Gen. DYSTHRENETA, n.g. (δυσθρηνητος, mournful.)

Palpi slender, ascending, recurved; second joint reaching base of antennae; terminal joint shorter, acute. Antennae without pecten; in male minutely ciliated. Forewings with 7 and 8 stalked, 7 to termen. Hindwings lanceolate; neuration normal.

2165. DYSTHRENETA LEPTA, n. sp. (λεπτος, tiny.)

♂, ♀. 9–10 mm. Head and thorax whitish sprinkled with fuscous; face white. Palpi whitish. Antennae whitish annulated with blackish. Abdomen fuscous; tuft whitish. Forewings narrow, costa gently arched, apex pointed, termen oblique; whitish uniformly sprinkled with fuscous; obscure fuscous dots on costa at base, middle, and before apex; a dot on tornus; cilia whitish with fuscous points. Hindwings and cilia grey-whitish.

North Queensland: Kuranda in September; four specimens.

182. Gen. DELOPHANES, n.g. (δηλοφανης, conspicuous.)

Tongue present. Palpi with second joint reaching base of antennae, slightly rough anteriorly; terminal joint 1, as stout as second, slightly rough anteriorly. Antennae with basal pecten; ciliations in male extremely minute. Forewings with 7 to termen. Hindwings lanceolate; 3 and 4 connate, 5 from below middle of cell.

Characterized chiefly by the palpi and hindwings. The exact affinities of this genus are doubtful.

2166. DELOPHANES ANTHRACEPHALA Low.

Trans. Roy. Soc. S. Aust., 1894, p. 105.

♂, ♀. 14–16 mm. Head and palpi blackish. Antennae blackish. Thorax white. Abdomen pale grey. Legs fuscous; posterior pair whitish. Forewings narrow, costa

gently arched, apex round-pointed, termen very oblique; white; markings blackish; a broad sub-basal fascia, biconcave, extending on costa from base to one-third, on dorsum much narrower; a similar fascia at apex, extending from three-fifths costa to apex and both sides of tornus; a white costal subapical dot; cilia white, on tornus fuscous. Hindwings broadly lanceolate; grey; cilia grey.

Queensland: Duaringa; Brisbane in December, Toowoomba in November; four specimens, including Lower's type. Lower gives Sydney as his locality, but this is probably an error. His type is labelled "Duaringa".

183. Gen. EUTORNA Meyr.

Trans. N.Z. Inst. 1889, p. 157.

Palpi ascending, recurved, long, smooth; second joint much exceeding base of antennae; thickened with appressed scales, sometimes rough or tufted at apex; terminal joint much shorter than second, slender, acute. Antennae without pecten; in male simple. Forewings with 7 and 8 stalked, 7 to costa, 6 sometimes to apex. Hindwings lanceolate; 5 curved, usually approximated to 4 at origin, sometimes to 6 after origin. Type, *E. caryochra* Meyr. from New Zealand. In addition to the twelve Australian species there are two from New Zealand, one from India, and one from Africa.

2167. EUTORNA LEPTOGRAPHA Meyr., *Trans. Roy. Soc. S. Aust.*, 1906, p. 41. (Bunya Mts., Ebor, Moe, Tasmania.)

2168. EUTORNA INTONSA Meyr., ibid., 1906, p. 42. (Macpherson Rge., Sydney, Gisborne, Melbourne, Healesville, Sale, Campbelltown, Tasm.)

2169. EUTORNA TRICASIS Meyr., ibid., p. 42. (Atherton, Nambour to Victoria, Macpherson Rge., Ebor, Mt. Wilson.)

2170. EUTORNA EUGRAMMA Meyr., ibid., 1906, p. 43. (Ebor, Mt. Wilson, Mt. Kosciusko, Victoria, Tasmania.)

2171. EUTORNA PABULICOLA Meyr., ibid., 1906, p. 43. (Cairns to Victoria.)

2172. EUTORNA SPINTHERIAS Meyr., ibid., 1906, p. 44. (Mt. Wilson, Gisborne, Beaconsfield, Healesville, Launceston, Deloraine.)

2173. EUTORNA DIAULA Meyr., ibid., 1906, p. 45. (Victoria, Casterton, Tasmania.)

2174. †EUTORNA EPICNEPHES Meyr., ibid., 1906, p. 46. (Brisbane, Sydney, Warragul.)

2175. EUTORNA PHACELOCOSMA Meyr., ibid., 1906, p. 45. (Eungella, Yeppoon, Mt. Tamborine, Macpherson Rge., Bunya Mts., Mt. Kosciusko, Tasmania.)

2176. EUTORNA PHILOGENES Meyr., ibid., 1906, p. 45. = *tapinopa* Turn., ibid., 1917, p. 17. (Caloundra, Brisbane, Mt. Tamborine, Macpherson Rge., Tyringham, Healesville.)

2177. EUTORNA DYSPHANES, n. sp. (δυσφανης, inconspicuous.)

♂, ♀. 12-13 mm. Head and thorax fuscous. Palpi with second joint slender, terminal joint three-fifths; ochreous-whitish, apex of second and base of terminal joint fuscous. Antennae fuscous. Abdomen grey. Legs ochreous-whitish; anterior fuscous with whitish tarsal rings. Forewings with costa gently arched, apex rounded, termen obliquely rounded; fuscous; a suffused darker line from three-fourths costa to tornus; some ochreous-whitish costal suffusion beyond middle; a dark fuscous line on apical fourth of costa and on termen; cilia ochreous-whitish, on tornus grey. Hindwings ochreous-whitish suffused with grey towards apex; cilia grey.

Queensland: Bunya Mts. in November and December; three specimens.

2178. EUTORNA PLUMBEOLA, n. sp. (*plumbeolus*, leaden.)

♂, ♀. 14-17 mm. Head, antennae and thorax fuscous. Palpi with second joint much thickened with appressed scales, terminal joint slender; fuscous; terminal joint with basal and median whitish rings. Abdomen grey. Legs fuscous with whitish rings. Forewings narrow, costa gently arched, termen very obliquely rounded; leaden-grey; stigmata fuscous, first discal at one-third, plical beyond it, second discal at two-thirds, sometimes a line between discals; cilia grey. Hindwings and cilia pale grey.

Western Australia: Albany and Denmark in March (W. B. Barnard); ten specimens. Type in Queensland Museum.

184. Gen. MACROBELA, n.g. (μακροβελος, with long palpi.)

Palpi porrect; second joint very long, thickened with rough scales above and beneath; terminal joint moderate, obtuse. Antennae without pecten; in male simple. Posterior tibiae smooth with some hairs on dorsum. Forewings with 2 from two-thirds, 3 from angle, 4 separate, 7 and 8 stalked, 7 to apex. Hindwings ovate; 5 approximated to 6 at origin.

2179. MACROBELA APREPTA, n. sp. (απρεπτος, unadorned.)

♂. 29 mm. Head, thorax, palpi, and antennae fuscous. Abdomen grey-whitish with fuscous bars. Legs fuscous; posterior pair whitish. Forewings elongate, costa moderately arched, apex rounded, termen straight; oblique; ochreous-whitish sprinkled with fuscous; a fuscous costal streak from base nearly to apex; another streak on fold; a longitudinal median streak from middle to three-fourths; cilia ochreous-whitish. Hindwings and cilia grey-whitish.

Western Australia: Perth in August; one specimen received from Mr. W. M. Matthews.

185. Gen. HETEROCHYTA Meyr.

Trans. Roy. Soc. S. Aust., 1906, p. 47.

Palpi very long, porrect; second joint very long, thickened with dense rough scales above and beneath; terminal joint much shorter, slender, pointed. Antennae without pecten; in male simple. Posterior tibiae smooth with some hairs on dorsum. Forewings with 2 from two-thirds, 7 and 8 stalked; 7 to apex. Hindwings elongate-ovate; 5 from middle of cell. Type, *H. xenomorpha* Meyr.

2180. HETEROCHYTA ASTEROPA Meyr., *Trans. Roy. Soc. S. Aust.*, 1906, p. 48. (Sydney, Sale, Mt. Lofty, Waroona, Perth.)

2181. HETEROCHYTA PYROSEMA Low., PROC. LINN. Soc. N.S.W., 1899, p. 109, Meyr., *Trans. Roy. Soc. S. Aust.*, 1906, p. 48. (Broken Hill.)

2182. HETEROCHYTA XENOMORPHA Meyr., ibid., 1906, p. 48. (Perth.)

186. Gen. HETEROBATHRA Low.

Trans. Roy. Soc. S. Aust., 1901, p. 89, Meyr., *Gen. Ins. Oecoph.*, p. 150.

Palpi very long, ascending, recurved; second joint more than three times length of face, thickened with appressed scales, expanded at apex; terminal joint less than one-half second, slender, acute. Antennae without pecten; in male simple. Forewings with 2 from before angle; 7 and 8 stalked, 7 to apex. Hindwings elongate-ovate; neuration normal. Type, *H. xiphosema* Low.

2183. †HETEROBATHRA XIPHOSEMA Low., *Trans. Roy. Soc. S. Aust.*, 1901, p. 90. (Broken Hill.)

2184. †HETEROBATHRA BIMACULA Low., ibid., 1901, p. 90. (Broken Hill.)

2185. †HETEROBATHRA TETRACENTRA Meyr., ibid., 1906, p. 47. (Geraldton.)

2186. †HETEROBATHRA INFESTA Meyr., *Exot. Micro.*, ii, p. 383. (Melbourne.)

2187. HETEROBATHRA CATORYCTOPSIS Low., *Trans. Roy. Soc. S. Aust.*, 1893, p. 184. (Mt. Lofty.)

187. Gen. ENCHOCRATES Meyr.

PROC. LINN. Soc. N.S.W., 1882, p. 442.

Palpi very long, porrect; second joint very long; much thickened with dense rough scales above and beneath; terminal joint short, slender, acute. Antennae without pecten. In male simple. Forewings with 2 from before angle, 7 and 8 stalked 7 to costa. Hindwings ovate; 5 curved and approximated to 4 at origin. Type, *E. glaucopis* Meyr.

2188. †ENCHOCRATES VESPERASCENS Meyr., *Exot. Micro.*, ii, p. 390. (Adelaide.)

2189. ENCHOCRATES PICROPHYLLA Meyr., PROC. LINN. Soc. N.S.W., 1886, p. 827. = sorentis Meyr., ibid., 1887, p. 929. (Sydney, Mt. Lofty.)

2190. ENCHOCRATES GLAUCOPIS Meyr., ibid., 1882, p. 443. (Stanthorpe, Sydney, Victoria.)

2191. †ENCHOCRATES PHAEDRYNTIS Meyr., ibid., 1887, p. 929. (Albany, Collie.)

188. Gen. EUPSELIA Meyr.

PROC. LINN. SOC. N.S.W., 1880, p. 132. *Trans. Roy. Soc. S. Aust.*, 1906, p. 38.

Palpi, ascending, recurved, smooth, slender, short; second joint reaching middle of face; terminal joint one-half second, pointed. Antennae without pecten; in male simple or with minute ciliations. Forewings with 7 and 8 coincident. Hindwings elongate-ovate; neuration normal. Type, *E. satrapella.* Sixteen Australian and one Indian species.

2192. EUPSELIA MELANOSTREPTA Meyr., PROC. LINN. Soc. N.S.W., 1880, p. 223. (Tweed Hds., Stanthorpe, Tenterfield, Glen Innes, Gisborne, Melbourne, Beaconsfield, Hobart, Mt. Lofty, Waroona.)

2193. EUPSELIA THEORELLA Meyr., ibid., 1880, p. 222. (Brisbane, Warwick, Stanthorpe, Cunnamulla, Sydney.)

2194. †EUPSELIA PERCUSSANA Walk., xxx, p. 998. Meyr., PROC. LINN. SOC. N.S.W., 1880, p. 219. (Tasmania.)

2195. EUPSELIA SATRAPELLA Meyr., ibid., 1880, p. 220. = *iridozona* Low., ibid., 1899, p. 115. (Brisbane to Victoria, Stanthorpe, Ebor, Charleville, Launceston, Cunderdin.)

2196. EUPSELIA BELTERA, n. sp. (βέλτερος, better.)

♂. 18 mm. Head and palpi yellow. Antennae grey. Thorax fuscous; anterior and posterior spots and apices of tegulae yellow. Abdomen fuscous; apices of segments yellowish. Legs fuscous with whitish-ochreous tarsal rings; posterior pair except tarsi yellow. Forewings gently arched, apex rounded, termen obliquely rounded; yellow; costa to middle suffused with fuscous; a fuscous terminal blotch containing long whitish longitudinal striae preceded by two transverse iridescent purple streaks; a yellow dot on costa before apex, and another minute dot on dorsum at three-fourths; five blackish dots on lower half of termen, of which alternate three are partly edged with brilliant gold; cilia fuscous, on costa yellow. Hindwings with termen gently rounded; yellow; margin around apex fuscous; cilia fuscous. Near *E. satrapella,* differing chiefly in the hindwings.

Queensland: Charleville in September; one specimen.

2197. EUPSELIA AXIEPAENA, n. sp. (ἀξιέπαινος, praiseworthy.)

♂. 11-12 mm. Head grey; face whitish. Palpi whitish. Antennae whitish with fuscous annulations. Thorax fuscous; tegulae more or less whitish. Legs fuscous; posterior pair whitish. Forewings with costa gently arched, apex rounded, termen obliquely rounded; pale yellow; markings fuscous; a moderate straight-edged basal patch; several fine short strigulae from costa; a large sharply defined apical patch, its edge nearly straight; cilia fuscous. Hindwings and cilia grey.

Queensland: Toowoomba in January (W. B. Barnard); two specimens. Type in Queensland Museum.

2198. EUPSELIA CALLIDYAS Meyr., *Exot. Micro.*, i, p. 306. (Darwin.)

2199. EUPSELIA PHILOMORPHA Low., PROC. LINN. SOC. N.S.W., 1901, p. 670. = *leucaspis* Meyr., *Trans. Roy. Soc. S. Aust.*, 1906, p. 38. (Stawell, Sea Lake, Quorn, York, Cunderdin.)

2200. EUPSELIA ANOMMATA Turn., ibid., 1898, p. 204. (Brisbane, Milmerran, Sydney.)

2201. †EUPSELIA SYNCAPNA Meyr., *Exot. Micro.*, ii, p. 317. (Brisbane.)

2202. EUPSELIA CARPOCAPSELLA Wlk., xxx, p. 998. Meyr., PROC. LINN. SOC. N.S.W., 1880, p. 219. = *beatella* Wlk., xxx, p. 999. Meyr., PROC. LINN. Soc. N.S.W., 1880, p. 219. = *holoxantha* Low., *Trans. Roy. Soc. S. Aust.*, 1894, p. 105. (Cape York to Hobart, Talwood, Birchip, Cradle Mt., Mt. Lofty, Western Australia.)

2203. EUPSELIA ARISTONICA Meyr., PROC. LINN. SOC. N.S.W., 1880, p. 218. (Emerald, Dalby, Sydney, Gisborne, Cradle Mt., Mt. Wellington, Adelaide, Goolwa.)

2204. EUPSELIA METABOLA, n. sp. (μεταβολος, variable.)

♂, ♀. 13-16 mm. Head fuscous. Palpi whitish, towards apex fuscous. Antennae fuscous. Thorax fuscous, tegulae more or less whitish. Abdomen fuscous, sometimes partly ochreous; sometimes whitish at base. Legs fuscous with whitish rings; posterior tibiae whitish. Forewings with costa slightly arched, apex rounded, termen obliquely rounded; fuscous; basal area white with fuscous transverse strigulae; a white spot

with a transverse fuscous strigula on costa beyond middle; sometimes the white basal area is extended to become confluent with costal spot; a white dot on costa before apex; several leaden-grey transverse lines in median area; subterminal area more or less sprinkled with very slender whitish scales; terminal edge brilliant metallic rosy-purple; a blackish spot encircled by metallic lustre on termen above tornus; cilia fuscous. Hindwings fuscous with a basal ochreous patch of variable size, in one example absent; cilia pale ochreous.

Queensland: Emerald in September; Dalby, Injune in June; Talwood; Stanthorpe in October. South Australia: Adelaide in October. Western Australia: Perth in December. Seven specimens. Type in Queensland Museum.

2205. †EUPSELIA TRISTEPHANA Meyr., *Exot. Micro.*, i, p. 306. (Darwin.)

2206. †EUPSELIA TRITHRONA Meyr., *Trans. Roy. Soc. S. Aust.*, 1906, p. 39. (Sydney.)

2207. †EUPSELIA HYPSICHORA Meyr., ibid., 1906, p. 39. (Victoria, Western Australia, York.)

189. Gen. PROGONICA, n.g. (προγονικος, ancestral.)

Palpi ascending, recurved, slender; second joint not reaching base of antennae; terminal joint one-half; pointed. Antennae without pecten; ciliations in male very short. Forewings with 7 and 8 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal. Closely allied to *Eupselia*; differing in the presence of vein 7 in the forewings.

2208. PROGONICA NIPHOSTIBES, n. sp. (νιφοστιβης, thick with snow.)

♂, ♀. 16–18 mm. Head, thorax, and palpi white. Antennae white with fuscous annulations; ciliations in male one-third. Abdomen grey. Forewings with costa gently arched, apex obtuse, termen slightly rounded, oblique; a basal white patch extending to two-fifths costa and dorsum, with slender fuscous costal strigulae; beyond this, fuscous; a triangular white spot on three-fourths dorsum; a white line from costa near apex to midtermen; preceded by a brown line, and followed by a brown apical spot; several rosy-purple metallic lines in posterior dark area; cilia white, below middle and on apex fuscous.

Queensland: Stanthorpe in December and January (W. B. Barnard); two specimens. Type in Queensland Museum.

190. Gen. SEMIOSCOPIS Hb.

Verz., p. 402. Meyr., *Gen. Ins. Oecoph.*, p. 186.

Palpi ascending, recurved, smooth; second joint long; terminal joint much shorter, acute. Antennae without pecten; in male shortly ciliated. Forewings with tufts of scales; 7 and 8 stalked, 7 to apex. Hindwings ovate; neuration normal. A small North American and European genus. Type, *S. avellanella* Hb. from Europe.

2209. SEMIOSCOPIS LIVIDELLA Meyr., PROC. LINN. SOC. N.S.W., 1883, p. 535. (Mt. Macedon.)

191. Gen. BARANTOLA Wlk.

xxix, p. 816. Meyr., PROC. LINN. SOC. N.S.W., 1904, p. 396.

Palpi long, ascending, recurved; second joint exceeding base of antennae, smooth, slender; terminal joint as long as second, slender, acute. Antennae longer than forewings; with pecten; in male simple. Forewings with 2 and 3 stalked or separate, 7 and 8 stalked, 7 to termen. Hindwings elongate-ovate; 5 from middle of cell. Type, *B. pulcherrima*.

2210. BARANTOLA PULCHERRIMA Wlk., xxix, p. 816. Meyr., PROC. LINN. SOC. N.S.W., 1904, p. 396. = *uranaula* Meyr., ibid., 1886, p. 1040. (Cape York to Lismore, Macpherson Rge., New Guinea.)

2211. BARANTOLA PANARISTA Turn., *Proc. Roy. Soc. Qd.*, 1917, p. 100. (Mt. Tamborine, New Guinea.)

192. Gen. SCORPIOPSIS Turn.

Trans. Roy. Soc. S. Aust., 1894, p. 132.

Palpi very long, ascending, recurved; second joint more than three times length of face, moderately thickened with smoothly appressed scales; terminal joint half second,

with a posterior subapical tuft more or less developed, moderately stout, acute. Antennae without pecten; in male simple. Forewings with 2 and 3 separate or stalked, 7 and 8 stalked, 7 to apex. Hindwings with 5 curved towards 4 at origin, 6 and 7 somewhat approximated at origin, gradually diverging. Monotypical.

2212. SCORPIOPSIS PYROBOLA Meyr., Proc. Linn. Soc. N.S.W., 1888, p. 1041. Ibid., 1888, p. 1041. = superba Turn., Trans. Roy. Soc. S. Aust., 1894, p. 133. (Cape York to Newcastle, Macpherson Rge., Bunya Mts.)

2213. SCORPIOPSIS RHODOGLAUCA Meyr., Exot. Micro., iii, p. 620. (Cairns, Atherton.)

193. Gen. BLEPTOCHITON, n.g. (βλεπτοχιτων, conspicuous.)

Palpi long, ascending, recurved; second joint much exceeding base of antennae thickened with smoothly appressed scales; terminal joint shorter than second, rather stout, acute. Antennae without pecten; in male simple. Anterior tibiae dilated towards apex. Forewings with 7 and 8 stalked, 7 to termen. Hindwings broadly ovate; 5 from below middle of cell.

2214. BLEPTOCHITON LEUCOTRIGONA, n. sp. (λευκοτριγωνος, with white triangle.)

♂, ♀. 24-26 mm. Head, thorax, and antennae grey. Palpi grey; inner surface whitish. Abdomen fuscous; apices of segments whitish-ochreous. Legs whitish-ochreous, midtarsi with fuscous rings. Forewings suboblong, costa gently arched, apex rectangular, termen slightly rounded, not oblique; grey sometimes partly reddish; a triangular snow-white costal spot beyond middle; stigmata fuscous, first discal at one-fourth, plical beyond it, second discal at one-half, narrowly lunate; a dark Y-shaped suffusion from tornus enclosing costal triangle; subterminal area pale, purple-tinged, containing a transverse series of longitudinal transverse streaks; a fuscous terminal line preceded by a pale line; cilia grey. Hindwings fuscous with a large yellow costal triangle; cilia yellow, towards tornus grey.

North Queensland: Eungella in October. Queensland: Bunya Mts. in November (W. B. Barnard); eleven specimens.

194. Gen. PSOROSTICHA Low.

Trans. Roy. Soc. S. Aust., 1901, p. 91. Meyr., Gen. Ins. Oecoph., p. 168.

Palpi ascending, recurved; second joint much exceeding base of antennae, much thickened with dense scales, rough anteriorly; terminal joint shorter, stout, acute. Antennae with weak pecten; in male simple. Forewings with 2 and 3 stalked, 7 and 8 stalked, 7 to costa. Hindwings elongate-ovate; 5 approximated to 4 at origin. Type, P. zizyphi Stn., Trans. Ent. Soc., 1859, p. 115. There is a second Indian species.

2215. PSOROSTICHA ZIZYPHI Stn., Trans. Ent. Soc., 1859, p. 115. = angusta Wlsm. Moore, Lep. Ceyl., iii, p. 508. = acrolopha Low., Trans. Roy. Soc. S. Aust., 1901, p. 92. (Cooktown, Townsville, Brisbane, Archipelago, Ceylon, India. Larvae on Citrus. Probably introduced.)

195. Gen. NEOSIGALA Turn.

Trans. Roy. Soc. S. Aust., 1917, p. 118.

Palpi long, ascending, recurved; second joint two and a half times length of face, moderately thickened with appressed scales. Antennae without pecten; in male minutely ciliated. Posterior tibiae hairy. Forewings with 2 and 3 stalked, 7 and 8 stalked, 7 to costa. Hindwings elongate-ovate; 5 approximated to 4 at origin. Monotypical.

2216. NEOSIGALA CEROPLASTA Turn., Trans. Roy. Soc. S. Aust., 1917, p. 118. (Mt. Tamborine.)

196. Gen. SCORPIOPSIS Turn.

Trans. Roy. Soc. S. Aust., 1894, p. 132. Meyr., Gen. Ins. Oecoph., p. 161.

Palpi very long, ascending, recurved; second joint more than three times length of face, moderately stout, smooth-scaled; terminal joint, shorter, acute, usually with a posterior tuft before apex. Antennae without pecten; in male simple. Forewings with 7 and 8 stalked, 7 to apex. Hindwings ovate; 7 curved downwards to approach 6, then

receding to near apex. The tuft on terminal joint of palpi is large in *S. pyrobola*, small in *S. superba*, absent in *S. rhodoglauca*. Type, *S. superba*. Three species have been recorded from New Guinea.

2217. SCORPIOPSIS SUPERBA Turn., *Trans. Roy. Soc. S. Aust.*, 1894, p. 133.

Differs from *S. pyrobola* in the more strongly rounded costa and apex of forewings, their white costal edge, and the differently arranged white spots. (Cape York, Yeppoon, Brisbane, Rosewood, Toowoomba.)

2218. SCORPIOPSIS PYROBOLA Meyr., PROC. LINN. SOC. N.S.W., 1886, p. 1041. (Macpherson Rge., Lismore, Newcastle.)

2219. SCORPIOPSIS RHODOGLAUCA Meyr., *Exot. Micro.*, iii, p. 620. (Cairns, Atherton.)

197. Gen. THUDACA Wlk.

xxix, p. 825. Meyr., PROC. LINN. SOC. N.S.W., 1892, p. 569. *Trans. Roy. Soc. S. Aust.*, 1906, p. 49.

Head with dense tuft of hairs on crown. Palpi ascending, recurved; second joint with appressed scales, reaching base of antennae; terminal joint shorter than second, slender, acute. Antennae without pecten or with a few scales only; in male simple, thickened. Forewings with 7 and 8 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal. Type, *T. obliquella* Wlk. Fifteen species. In males of *T. crypsidesma*, *T. mimodora* and *T. haplonota* the face is excavated anteriorly and the palpi have shortened second and minute terminal joints.

2220. †THUDACA HETERASTIS Meyr., PROC. LINN. SOC. N.S.W., 1892, p. 571. (Geraldton.)

2221. THUDACA CAMPYLOTA Meyr., ibid., 1892, p. 572. (Nornalup, Bridgetown, Perth.)

2222. THUDACA CRYPSIDESMA Meyr., ibid., 1892, p. 572. (Melbourne, Gisborne, Cradle Mt., Strahan, Mt. Lofty, Pt. Lincoln, Perth.)

2223. THUDACA HAPLONOTA Meyr., ibid., 1892, p. 573. *Gen. Ins. Oecoph.*, Pl. v, fig. 100. (Denmark, Waroona, Perth, Yanchep, Geraldton.)

2224. THUDACA MIMODORA Meyr., ibid., 1892, p. 574. (Caloundra to Sydney, Ebor, Katoomba, Mt. Kosciusko, Mt. Buffalo, L. St. Clair.)

2225. THUDACA OBLIQUELLA Wlk., xxix, p. 825. Meyr., ibid., 1892, p. 575. (Atherton, Nambour to Victoria, Katoomba, Tasmania, Mt. Lofty, Kangaroo I.)

2226. THUDACA MONOLECHRIA, n. sp. (μονολεχριος, with one oblique line.)

♀. 16 mm. Head and thorax orange-yellow. Palpi whitish. Antennae grey. Abdomen and legs whitish. Forewings with costa strongly arched, apex acute, termen straight, oblique; shining white; markings orange-yellow; a broad costal streak from base almost to apex; leaving costal edge white; a dorsal streak throughout; a line from apex to three-fourths dorsum; cilia yellow. Hindwings and cilia whitish-grey.

North Queensland: Cape York in October (W. B. Barnard); two specimens. Type in Queensland Museum.

2227. THUDACA RUBRILINEA, n. sp. (*rubrilineus*, red-lined.)

♂. 22 mm. Head fuscous. (Palpi missing.) Antennae whitish. Thorax reddish-orange, posterior spot and inner edge and apex of tegulae white. Abdomen whitish. Legs fuscous; posterior pair whitish. Forewings narrow, costa slightly arched, apex obtuse, termen obliquely rounded; shining white; a broad reddish-orange costal line from base to apex; a similar dorsal line from near base to tornus and thence continued to near apex; cilia reddish-orange, on tornus grey-whitish. Hindwings whitish-grey; cilia whitish.

Western Australia: Cunderdin in November (R. Illidge); one specimen.

2228. THUDACA CALLIPHROTIS Meyr., PROC. LINN. SOC. N.S.W., 1892, p. 576. (Geraldton.)

2229. THUDACA CYMATISTIS Meyr., ibid., 1892, p. 577. (Carnarvon.)

2230. THUDACA OPHIOSEMA Meyr., ibid., 1892, p. 576. (Geraldton.)

2231. THUDACA STADIAULA Meyr., ibid., 1892, p. 578. (Geraldton.)

2232. THUDACA ORTHODROMA Meyr., ibid., 1892, p. 577. (Geraldton.)

2233. THUDACA TRABEATA Meyr., ibid., 1892, p. 578. (Noosa and Stanthorpe to Victoria and Tasmania, Mt. Kosciusko, Mt. Lofty, Western Australia.)

2234. THUDACA CIRCUMDATELLA Wlk., xxx, p. 1012. Meyr., ibid., 1892, p. 571. (Brisbane, Sydney, Pt. Macquarie.)

2235. THUDACA CRYEROPIS, n. sp. (κρυερωπις, icy.)

♂. 22 mm. Head, thorax, palpi, abdomen and legs white. Forewings with costa rather strongly arched, apex pointed, termen straight, oblique; shining white; cilia white. Hindwings and cilia white.

• New South Wales: Maryland near Stanthorpe in December; one specimen.

2236. THUDACA INNUBILA Turn., *Proc. Roy. Soc. Tasm.*, 1926, p. 154. (Tasmania.)

2237. THUDACA LITODES, n. sp. (λιτωδης, smooth.)

♂, ♀. 18–24 mm. Head, thorax, and antennae grey-whitish. Palpi, abdomen and legs white. Forewings narrow-oblong, costa gently arched, apex rounded-rectangular, termen obliquely rounded; ochreous-whitish; cilia white. Hindwings and cilia white.

Queensland: Emerald in September (W. B. Barnard); five specimens. Type in Queensland Museum.

198. Gen. ACRAEPHNES, n.g. (ἀκραιφνης, pure, unmarked.)

Head loosely scaled, but without erect tuft. Palpi ascending, recurved; second joint reaching but scarcely exceeding base of antennae, smooth, slender; terminal joint short, slender, acute. Antennae without pecten; in male minutely ciliated. Forewings with 7 and 8 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal. Allied to *Thudaca*, but differs in the absence of cephalic tuft. Type, *A. nivea*.

2238. ACRAEPHNES NIVEA, n. sp. (*niveus*, snow-white.)

♂, ♀. 16–22 mm. Head and thorax white or grey-whitish. Palpi, antennae, abdomen and legs white. Forewings rather narrow, costa gently arched, apex round-pointed, termen obliquely rounded; white; cilia white. Hindwings and cilia white.

Queensland: Rockhampton in June; Emerald in September and April; Stanthorpe in February. New South Wales: Tenterfield in March; Brunswick Hds. in January. Eleven specimens.

2239. ACRAEPHNES NITIDA, n. sp. (*nitidus*, shining.)

♂, ♀. 16–20 mm. Head and thorax grey or whitish-grey. Palpi, antennae, abdomen and legs white. Forewings with costa moderately or strongly arched, apex pointed, termen very oblique; shining white; cilia white. Hindwings and cilia white.

Western Australia: Waroona in January (W. B. Barnard); three specimens.

199. Gen. ANALCODES, n.g. (Weak.)

Palpi smooth, slender, ascending, recurved; second joint reaching base of antennae; terminal joint shorter, acute. Antennae with pecten; in male stout, simple. Forewings with 7 and 8 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal.

2240. ANALCODES HYPERCHYTA, n. sp. (ὑπερχυτος, much suffused.)

♂. 14 mm. Head, thorax and abdomen fuscous. Palpi whitish mixed with fuscous. Antennae whitish-ochreous. Legs fuscous with whitish rings; posterior pair mostly whitish. Forewings with costa moderately arched, apex round-pointed, termen obliquely rounded; dark fuscous largely suffused with ochreous-whitish; a large pale basal blotch extending to midcosta and one-fourth dorsum; a dot on two-thirds dorsum; a spot on three-fourths costa, giving off a short line towards tornus; cilia dark fuscous. Hindwings and cilia fuscous.

New South Wales: Mt. Wilson in November; one specimen.

200. Gen. HAERETA, n.g. (αἱρετος, picked out.)

Palpi ascending, recurved, very long, smooth, slender; second joint three times length of face; terminal joint much shorter (one-third), acute. Antennae without pecten; in male simple. Forewings with 7 and 8 stalked, 7 to termen. Hindwings elongate-ovate; neuration normal. Type, *H. cryphimaea*.

2241. HAERETA NIPHOSCELES, n. sp. (νιφοσκελης, white-legged.)

♂. 16 mm. Head and thorax fuscous; face ochreous-whitish. Palpi with terminal joint one-third; fuscous. Antennae and abdomen pale grey. Anterior legs snow-white

with two blackish tarsal rings; middle pair pale greyish; posterior pair ochreous-whitish. Forewings with costa moderately arched, apex subrectangular, termen straight, oblique; 7 to termen; rosy; stigmata fuscous, first discal at one-fourth; plical beyond it, second discal near middle; an interrupted dark fuscous terminal line continued on apical fourth of costa; cilia rosy, apices pale grey. Hindwings and cilia white.

North Queensland: Lake Barrine, Atherton Tableland, in September; one specimen.

2242. HAERETA INSCRIPTA, n. sp. (*inscriptus*, scribbled.)   •

♂. 19 mm. Head, thorax, and abdomen white. (Palpi missing.) Antennae whitish. Legs whitish; anterior, pair fuscous; middle and posterior tibiae fuscous at base. Forewings narrow, costa strongly arched, apex acute, termen very oblique; 7 to termen; white; markings fuscous; some suffusion at bases of costa and dorsum; a median dot on fold; twin dots above middle at two-thirds; a small spot on costa near apex, connected by a zig-zag line with a dot above tornus; terminal dots on middle and beneath costa; cilia white. Hindwing and cilia white.

South Australia: Ooldea in October (W. M. Mathews); one specimen.

2243. HAERETA CRYPHIMAEA, n. sp. (κρυφιμαιος, secret.)

♂, ♀. 15–19 mm. Head and thorax brown. Palpi long; second joint about three times length of face, terminal joint one-third; brown, inner surface paler. Antennae brown finely barred with blackish on dorsum. Abdomen grey. Legs fuscous; anterior tarsi brown-whitish with blackish rings on bases of second and third joints; posterior pair brown-whitish. Forewings with costa moderately arched, apex rounded, termen obliquely rounded; 7 to termen; brown; stigmata blackish, first discal at one-fourth, plical beyond it, second discal at three-fifths, transversely elongate or double; a subcostal series of minute dots from two-thirds, curved in disc to end on dorsum before tornus; a terminal series of dots; cilia brown, apices whitish. Hindwings whitish with slight grey suffusion towards apex; cilia whitish.

Queensland: Mt. Tamborine in November; Macpherson Rge. in December and January; twelve specimens.

201. Gen. BRACHYZANCLA, n.g. (βραχυζαγκλος, with short sickles.)

Palpi ascending, recurved; second joint reaching or slightly exceeding base of antennae, slightly or moderately thickened with appressed scales; terminal joint shorter, slender, acute. Antennae without pecten; in male simple or minutely ciliated. Forewings with 7 and 8 stalked, 7 to costa or apex or rarely to termen. Hindwings elongate-ovate; neuration normal. Differs from *Cryptolechia* in its shorter palpi. Most of the species are relatively small. Type, *B. poenicea.* Eight species.

2244. BRACHYZANCLA POENICEA, n. sp. (*poeniceus*, reddish.)

♂. 16 mm. Head and thorax fuscous. Palpi fuscous, inner surface and extreme apex whitish. Antennae fuscous. Abdomen grey; tuft whitish-ochreous. Legs fuscous; posterior pair whitish. Forewings narrow, costa gently arched, apex rounded, termen obliquely rounded; 7 to costa; dull ochreous-reddish; stigmata minute, fuscous, first discal at two-fifths, plical slightly beyond it, second discal at two-thirds; minute fuscous dots on apical third of costa; cilia whitish-grey. Hindwings and cilia whitish-grey.

Queensland: Bunya Mts. in March; one specimen.

2245. BRACHYZANCLA SPORIMA, n. sp. (σποριμος, sprinkled.)

♂, ♀. 14–16 mm. Head and thorax whitish-ochreous with a few blackish scales. Palpi whitish-ochreous with blackish irroration more pronounced on terminal joint. Antennae whitish-ochreous annulated with blackish; in male slightly serrate and minutely ciliated. Abdomen ochreous-whitish. Legs ochreous-whitish; all tarsi and middle tibiae with dark fuscous rings; anterior pair mostly dark fuscous. Forewings with costa nearly straight, except at base and apex, apex rounded; 7 to costa; whitish-ochreous sparsely irrorated, especially towards margins, with large blackish scales; a small basal blackish fascia, moderate blackish discal spots at one-fourth and middle; cilia whitish-ochreous with a few blackish points. Hindwings grey-whitish; cilia whitish.

Queensland: Stanthorpe in October and November; five specimens taken at rest on granite rocks.

2246. BRACHYZANCLA ACROCROSSA, n. sp. (ἀκροκροσσος, with apical border.)

♂. 10-14 mm. Head fuscous; face ochreous-whitish. Palpi fuscous, internal surface ochreous-whitish. Antennae fuscous; in male thickened and slightly serrate. Thorax fuscous. Abdomen fuscous; tuft and underside whitish-ochreous. Legs fuscous; posterior pair whitish-ochreous. Forewings with costa rather strongly arched, apex rounded; 7 to costa; grey sprinkled with fuscous; apical third more strongly suffused with fuscous; two discal dots obscurely indicated at one-third and two-thirds, rarely another dot beneath the latter; a dark fuscous line or dotted chain along apical fourth of costa and around apex and upper part of termen; cilia whitish-brown. Hindwings pale grey, towards base whitish-ochreous; cilia pale grey with a whitish-ochreous basal line.

Queensland: Goodna, near Brisbane, in March; Toowoomba in October and December; four specimens.

2247. BRACHYZANCLA DYSGENES, n. sp. (δυσγενης, lowborn.)

♂. 12 mm. Head, thorax, and antennae pale grey. Palpi whitish. Abdomen pale grey; tuft whitish. Legs whitish. Forewings with costa moderately arched, apex rounded, termen obliquely rounded; 7 to costa; whitish with slight grey sprinkling; stigmata grey, minute, first discal at one-third, plical slightly beyond it, second discal before two-thirds; a terminal series of dots extending to apical third of costa; cilia whitish. Hindwings and cilia grey-whitish.

Queensland: Toowoomba in December; one specimen.

2248. BRACHYZANCLA LEPTODES, n. sp. (λεπτωδης, insignificant.)

♂. 13 mm. Head, thorax, and abdomen grey. Palpi grey, terminal joint and apex of second whitish. Antennae whitish-grey. Forewings narrow, costa moderately arched, apex pointed, termen obliquely rounded; 7 to apex; whitish with slight fuscous irroration; stigmata minute, fuscous, first discal at one-third, plical beyond it, second discal at two-thirds; terminal edge fuscous; cilia whitish. Hindwings and cilia pale grey.

Queensland: Macpherson Rge. (2,500 ft.) in November; one specimen.

2249. BRACHYZANCLA PLACOPHORA, n. sp. (πλακοφορος, blotched.)

♂. 14 mm. Head and thorax whitish. Palpi with second joint reaching base of antennae; fuscous, terminal joint whitish. Antennae fuscous; in male serrate, minutely ciliated. Abdomen and legs grey. Forewings with costa gently arched, apex obtuse, termen obliquely rounded; 7 to termen; white with some fuscous sprinkling; markings dark fuscous; a costal line from base to one-third; a spot on middle of dorsum; a large spot on two-thirds costa, connected with a short supramedian streak; an irregular apical spot; cilia whitish. Hindwings and cilia pale grey.

New South Wales: Lismore in October; two specimens.

2250. BRACHYZANCLA BAEA, n. sp. (βαιος, humble.)

♂. 22 mm. Head, thorax, and abdomen ochreous-whitish. Palpi with second joint moderately thickened, rough anteriorly; terminal short, slender, acute. Antennae grey. Legs ochreous-whitish, anterior pair fuscous. Forewings narrow, costa slightly arched, apex rounded; termen very oblique; 7 to apex; ochreous-whitish; cilia whitish. Hindwings narrowly elongate-ovate; whitish; cilia whitish.

New South Wales: Broken Hill in May; one specimen.

2251. BRACHYZANCLA ILLEPIDA Turn. *Proc. Roy. Soc. Tasm.*, 1926, p. 155. (Tasmania.)

202. Gen. TONICA Wlk.

xxix, p. 788. Meyr., *Gen. Ins. Oecoph.*, p. 167.

Palpi very long, ascending, recurved; second joint more than three times length of face, much thickened with long dense hairs beneath from one-third to apex and a short tuft above at one-third; terminal joint shorter, slender, acute, with rough hairs anteriorly and posteriorly in middle half. Antennae without pecten; in male simple. Anterior tibiae and tarsi short and broad; posterior tibiae densely hairy. Thorax with a large double posterior crest. Forewings with tufts of rough scales; 7 and 8 stalked, 7 to costa. Hindwings broad, subobliong; 5 approximated to 4 at origin. Type, *T. teratella* Walk. from India. An Indo-Malayan genus of which seven species have been recorded.

2252. TONICA EFFRACTELLA. Snel., *Tijd. v. Ent.*, 1879, p. 11. Meyr., *Trans. Roy. Soc. S. Aust.*, 1902, p. 164. (Darwin, Cape York to Mt. Tamborine.)

203. Gen. OCTASPHALES Meyr.

Trans. Roy. Soc. S. Aust., 1902, p. 161.

Palpi slender, ascending, recurved; second joint exceeding base of antennae; terminal joint slender, acute. Antennae without pecten; in male simple. Posterior tibiae smooth with a few rough scales on upper surface. Forewings with 2 from angle closely approximated or stalked with 3, 7 and 8 coincident. Hindwings broadly ovate; 5 approximated to 4 at origin. Type, *O. charitopa* Meyr. from New Guinea. Meyrick records two additional Papuan species.

2253. OCTASPHALES EUBROCHA Turn., *Trans. Roy. Soc. S. Aust.*, 1917, p. 120. (Brisbane, Stradbroke I., Tweed Hds., Toowoomba.)

2254. OCTASPHALES CHORDERES Meyr., ibid., 1902, p. 161. (Brisbane, Toowoomba, Rosewood, Tyringham.)

204. Gen. PERITORNEUTA Turn.

Trans. Roy. Soc. S. Aust., 1900, p. 13. Meyr., *Gen. Ins. Oecoph.*, p. 165.

Palpi very long, ascending, recurved, second joint more than three times length of face, smoothly thickened with appressed scales; terminal joint shorter than second, slender, smooth, acute. Antennae without pecten; in male simple. Forewings with 2 and 3 approximated at origin, 7 and 8 stalked, 7 to apex. Hindwings broadly ovate; 5 approximated to 4 at origin. Type, *P. circulatella* Wlk. Six species.

2255. PERITORNEUTA CIRCULATELLA Wlk., xxix, p. 767. Meyr., PROC. LINN. SOC. N.S.W., 1902, p. 162. (Townsville, Yeppoon, Maryborough to Lismore, Injune.)

2256. PERITORNEUTA LISSOPIS, n. sp. (λισσωπις, smooth.)

♀. 20–22 mm. Head and thorax leaden-grey. Palpi grey; terminal joint fuscous towards apex, extreme apex pale ochreous. Antennae grey-whitish annulated with blackish. Abdomen whitish-ochreous. Legs whitish with fuscous rings; posterior pair wholly whitish. Forewings with costa strongly arched, apex rounded, termen rounded, scarcely oblique; leaden-grey with numerous fuscous dots on veins; costal edge pale rosy; a small irregular brownish patch strigulated with fuscous on costa beyond middle, sometimes a similar sub-basal patch on dorsum; cilia grey-whitish. Hindwings and cilia whitish-ochreous.

Queensland: Duaringa; Jandowae, near Dalby; Injune in February; Bollon in April; four specimens.

2257. PERITORNEUTA MINANS Meyr., *Exot. Micro.*, ii, p. 391. (Brisbane.)

2258. PERITORNEUTA BACCHATA Meyr., ibid., i, p. 225. (Cape York to Sydney, Macpherson Rge.)

2259. PERITORNEUTA STIGMATIAS Turn., *Trans. Roy. Soc. S. Aust.*, 1900, p. 14. (Dunk I. to Tweed Hds., Bunya Mts., Macpherson Rge.)

2260. PERITORNEUTA THYELLIA Turn., ibid., 1902, p. 162. (Thursday I. to Newcastle, Bunya Mts., Macpherson Rge.)

2261. PERITORNEUTA RHODOPHANES Meyr., ibid., 1902, p. 162. (Perth, York, Geraldton.)

205. Gen. CRYPTOLECHIA Zel.

Lep. Micr. Caffr., 1852, p. 106. Meyr., *Gen. Ins. Oecoph.*, p. 195.

Head with loosely appressed scales, sometimes projecting over face. Palpi long, ascending, recurved; second joint three times length of face, somewhat thickened with appressed scales; terminal joint long, slender, acute. Antennae without pecten; in male simple or minutely ciliated. Forewings with 2 and 3 separate, 7 and 8 stalked, 7 to apex or costa. Hindwings elongate-ovate or broadly ovate; neuration normal. Type, *C. straminella* Zel. from Africa. Thirty Australian species. A genus of nearly one hundred species represented in all regions.

2262. CRYPTOLECHIA HUMERANA Wlk., xxviii, p. 366. Meyr., *Trans. Roy. Soc. S. Aust.*, 1902, p. 159. *Gen. Ins. Oecoph.*, Pl. vi, fig. 115. (Stanthorpe to Tasmania.)

2263. CRYPTOLECHIA LUTEA Turn., *Proc. Roy. Soc. Tasm.*, 1926, p. 154.

2264. CRYPTOLECHIA ARGILLEA Turn., ibid., 1926, p. 155.

2265. CRYPTOLECHIA HYPOXANTHA Low., PROC. LINN. SOC. N.S.W., 1897, p. 269. = *eumorpha* Meyr., *Trans. Roy. Soc. S. Aust.*, 1902, p. 159. (Stanthorpe, Armidale, Bowral, Broken Hill, Victoria.)

2266. CRYPTOLECHIA LEWINELLA Newm., *Trans. Ent. Soc.*, 1855, p. 291. = *neurosticha* Low., *Trans. Roy. Soc. S. Aust.*, 1894, p. 112. (Macpherson Rge., Toowoomba, Stanthorpe to Cooma, Gisborne, Tasmania, Mt. Lofty.)

2267. CRYPTOLECHIA COSMOPODA Turn., ibid., 1900, p. 12. = *tripunctella* Meyr., ibid., 1902, p. 12. (Nambour to Victoria, Bunya Mts., Stanthorpe.)

2268. CRYPTOLECHIA ANTHRACIAS Low., ibid., 1902, p. 246. (Healesville, Stawell, Birchip.)

2269. CRYPTOLECHIA RHODOMITA Turn. ibid., 1900, p. 13. (Mt. Tamborine.)

2270. CRYPTOLECHIA RHAPHIDIAS Turn., ibid., 1917, p. 119. (Brisbane.)

2271. CRYPTOLECHIA SARCINODES Meyr., *Exot. Micro.*, ii, p. 395. (Pinnaroo.)

2272. CRYPTOLECHIA TRIPUNCTELLA Wlk., xxix, p. 757. Turn., *Trans. Roy. Soc. S. Aust.*, 1917, p. 118. *nec* Meyr., ibid., 1902, p. 159. (Tasmania.)

2273. CRYPTOLECHIA EMPALACTA Meyr., *Exot. Micro.*, i, p. 305. (Mt. Kosciusko, Tasmania.)

2274. CRYPTOLECHIA CERAMORA Meyr., *Trans. Roy. Soc. S. Aust.*, 1902, p. 160. (Gisborne.)

2275. CRYPTOLECHIA RADIOSELLA Wlk., xxviii, p. 539. Meyr., *Trans. Roy. Soc. S. Aust.*, 1906, p. 48. (Sydney to Tasmania, Mt. Lofty, Western Australia.)

2276. CRYPTOLECHIA STRIATA. n. sp. (*striatus*, streaked.)

♂. 21 mm. Head, palpi and antennae fuscous. Thorax fuscous; tegulae grey. Abdomen and legs grey. Forewings very narrow; costa gently arched, apex pointed, termen very oblique; 7 to costa; whitish with fuscous lines on veins; these coalesce to form a longitudinal median streak from middle expanding towards apex, and another on fold from one-third to tornus; a whitish terminal line; cilia grey. Hindwings and cilia grey.

Queensland: Brisbane in February; one specimen.

2277. †CRYPTOLECHIA SCOLIA Meyr., *Trans. Roy. Soc. S. Aust.*, 1902, p. 155. (Sydney.)

2278. CRYPTOLECHIA ANTICROSSA Meyr., *Exot. Micro.*, i, p. 304. (Cape York.)

2279. CRYPTOLECHIA SCHISTOPA Meyr., *Trans. Roy. Soc. S. Aust.*, 1902, p. 156. (Yeppoon to Gisborne, Stanthorpe, Glen Innes.)

2280. CRYPTOLECHIA PYTINAEA Meyr., ibid., 1902, p. 157. (Stanthorpe, Sydney, Mittagong, Victoria, Albany.)

2281. †CRYPTOLECHIA PACHNIAS Meyr., ibid., 1902, p. 155. (Duaringa.)

2282. †CRYPTOLECHIA AMPHIGRAMMA Meyr., *Exot. Micro.*, i, p. 305. (Gosford.)

2283. †CRYPTOLECHIA MUNICIPALIS Meyr., ibid., ii, p. 316. (Brisbane.)

2284. CRYPTOLECHIA AMAUROPHANES, n. sp. (ἀμαυροφανής, obscure.)

♂. 22 mm. Head, thorax, palpi and abdomen grey. Abdomen whitish-grey. Legs whitish. Forewings elongate, costa moderately arched, apex rounded, termen obliquely rounded; 7 to costa; costal edge towards base tinged with pink; whitish sprinkled with fuscous, which tends to form streaks on veins; cilia whitish sprinkled with fuscous. Hindwings and cilia whitish-grey.

New South Wales: Murrurundi in October; one specimen received, Dr. B. L. Middleton.

2285. CRYPTOLECHIA CORIARIA Meyr., *Exot. Micro.*, i, p. 173. (Lorne, Mt. St. Bernard.)

2286. CRYPTOLECHIA EPINEPHELA, n. sp. (ἐπινεφελος, clouded.)

♂. 22–24 mm. Head pale grey; face with anteriorly projecting tuft from upper edge. Palpi very long, ascending, recurved; terminal joint two-thirds; pale grey, terminal joint and a subapical ring on second joint dark grey. Antennae grey. Thorax pale grey. Abdomen whitish-grey. Legs whitish-grey. Forewings suboblong, costa strongly arched, apex rounded-rectangular, termen obliquely rounded; 7 to costa; pale grey; a large

ill-defined grey blotch on tornal area from base to middle; stigmata grey, first discal at one-third, plical beneath it, second discal before two-thirds; a subcostal line of grey dots from middle, continued as subterminal line of dots; a terminal series of dots; cilia pale grey. Hindwings and cilia grey-whitish.

Queensland: Mt. Tamborine in October; Macpherson Rge. (3,000 ft.) in February; two specimens.

2287. CRYPTOLECHIA IROBELA, n. sp. (εἰροβελος, with woolly palpi.)

♂. 20 mm. Head, thorax, and abdomen whitish. Palpi with second joint two and a half times length of face, much thickened, rough anteriorly, terminal joint shorter, slender, acute; whitish. Antennae grey. Legs whitish; anterior pair fuscous. Forewings with costa gently arched, apex pointed, termen straight, oblique; 7 to costa; whitish with very scanty fuscous irroration; stigmata minute, fuscous, first discal at one-third, plical beyond it, second discal before two-thirds; some fuscous dots on termen and apical two-fifths of costa; cilia whitish. Hindwings and cilia whitish. Characterized by the peculiar palpi.

Western Australia: Kalamunda, near Perth, in December (W. B. Barnard); one specimen.

2288. CRYPTOLECHIA BRACHYMITA, n. sp. (βραχυμιτος, with short threads.)

♂. 21–22 mm. Head and thorax white. Palpi with second joint over 3, smooth; terminal joint shorter, slender, acute; white. Antennae fuscous. Legs fuscous; posterior pair whitish. Forewings narrow, costa gently arched, apex pointed, termen straight, oblique; 7 to costa; white with minute fuscous dots; first discal at one-fourth, second before two-thirds, plical represented by a short slender streak; sometimes a similar median streak before termen; a terminal series of dots continued on apical part of costa; cilia white. Hindwings and cilia white.

Western Australia: Perth in December and January (W. B. Barnard); two specimens. Type in Queensland Museum.

2289. CRYPTOLECHIA LEPTOSTICTA, n. sp. (λεπτοστικτος, with fine dots.)

♂, ♀. 18–20 mm. Head, thorax, palpi, and antennae whitish-ochreous. Antennae whitish. Legs whitish; anterior femora and flexor surface of tibiae fuscous. Forewings suboblong, costa gently arched, apex rectangular, termen slightly rounded, slightly oblique; ochreous-whitish with fine fuscous dots; a dot on base of fold; first discal at one-fourth, plical beyond it, sometimes two dots on end of cell; a subcostal series of dots beyond middle, recurved before apex to end above mid-dorsum; a series of dots on termen and apical part of costa; cilia whitish. Hindwings broadly ovate; whitish, cilia whitish.

North Queensland: Cooktown in April; Kuranda in November; Lake Barrine, Atherton Tableland, in September; three specimens.

2290. CRYPTOLECHIA INQUINATA, n. sp. (inquinatus, stained.)

♂. 14 mm. Head fuscous; face white. Palpi white; apex of second joint fuscous. Antennae, thorax, and abdomen fuscous. Legs whitish; anterior femora and tibia fuscous. Forewings suboblong, costa strongly arched, apex rectangular, termen slightly rounded, slightly oblique; whitish; markings fuscous, suffused; a basal patch extended on costa to two-fifths and along fold to dorsum; a costal spot at three-fifths; a short costal line running to apex; five slender lines running to termen; cilia whitish-ochreous. Hindwings broadly ovate; fuscous, cilia grey.

North Queensland: Kuranda (F. P. Dodd); one specimen.

2291. †CRYPTOLECHIA ALPHITIAS Low., Trans. Roy. Soc. S. Aust., 1923, p. 56. PROC. LINN. SOC. N.S.W., 1923, p. 56. (New South Wales: Dorrigo.)

SOME OBSERVATIONS ON THE CYTOLOGY OF OOGENESIS IN THE SYDNEY ROCK OYSTER (*OSTREA COMMERCIALIS* I. & R.).

By K. W. CLELAND.

(*From the Department of Anatomy, University of Sydney.*)

(Plates xvi-xx; four Text-figures.)

[Read 30th July, 1947.]

Contents.

I. INTRODUCTION.

This work was undertaken to provide (*a*) a morphological basis for future studies in cell physiology and (*b*) a cytological basis for studies on the histology of oyster gonads in relation to seasonal and sex cycles, etc., undertaken by the C.S.I.R. Marine Biological Laboratory, Cronulla, N.S.W., in their programme of oyster research.

In connection with the first aim, the ovaries and eggs of the locally available sea urchin *Heliocidaris* and the starfish *Patiriella* were examined. While cytologically interesting, they were not considered suitable for cell physiological studies, as, apart from the large size of the egg and the presence of large numbers of fat globules, the eggs were available for only a short period and the adults were difficult to maintain in the laboratory. Investigation showed that the eggs of the Sydney Rock Oyster were more satisfactory for physiological studies.

The taxonomic position of the animal appears to be somewhat confused. Iredale (1936) assigns it to a new genus *Saxostrea*. Thomson (1945) sees no reason for this split or for a departure from the genus *Ostrea* (possibly with subgeneric rank of *Gryphea*). Iredale and Roughley (1933) consider the animal to be a new species— *commercialis*. Prior to 1933 it was referred to *glomerata* or *cucullata*. Throughout this paper it will be referred to as *Ostrea commercialis*.

1. *Previous Literature on Pelecypod Oogenesis.*

No exhaustive search of the literature has been made, but the following observations of other workers on oogenesis were noted in the course of general reading on this subject.

Woods (1932) describes the ovary and mitochondria of the freshwater eulamellibranch *Sphaerium*. He finds a well-developed germinal membrane with nurse cells which were engulfed by the growing oocyte. The latter retains connection with the follicle wall by a stalk. The mitochondria, which are represented by a cloud of small granules, are at first perinuclear, but adopt a basal position as the stalk develops, and retain this position in the mature egg. They were considered to be germ cell

M

determinants in this animal and were segregated fairly completely in one cell of the blastula.

Okada (1934) describes the histology of oogenesis in the freshwater lamellibranch *Musculium heterodon*. He finds all stages of maturation in the ovary at the one time. The egg retains connection with the follicle wall by a stalk for a considerable time. The nucleus is distal and the nucleolus often multiple.

Rai (1930) worked on the Bombay oyster *Ostrea cucullata*. In the living egg, he describes clear spherical bodies and small granular bodies, neither of which stained with neutral red. The former were regarded as Golgi bodies and an apparent change in their composition was noted in eggs stained with osmium tetroxide—in the young eggs the bodies assumed a copper hue, while in the mature egg they became black. On this and other grounds he considers that neutral fat is laid down in them as oogenesis proceeds. The mitochondria which at first are small and perinuclear in position are larger and evenly distributed in the mature egg. Nucleolar extrusions are also described.

Subramaniam (1937) describes the cytoplasmic aspects of oogenesis in the Indian bivalve *Meretrix casta*. He finds the mitochondria first appearing on one side of the nucleus in early oocytes. They later become perinuclear, multiply, become more fuchsinophilic and are uniformly distributed in the mature egg. The Golgi bodies first appear in an oocyte larger than that in which the mitochondria first appear, and there is no nuclear concentration of these bodies at any time. From the first they appear as vesicles. Neutral red stains first the interior of the vesicle and there follows a diffuse staining of the cytoplasm around the vesicle. Subramaniam used normal saline (presumably mammalian) as a suspension medium. With further staining, neutral red vacuoles appear *de novo* in the cytoplasm. A similar vacuolation could be produced by alkaline water. Throughout oogenesis the nucleolus was forming buds which attached themselves to the nuclear membrane and diffused out. During this budding process the nucleolus sometimes showed vacuolation.

Worley (1944), using the mussel *Mytilis californianus*, finds the mature egg 50–70μ in diameter, orange in colour and having a well-developed endoplasm-cortex differentiation. In the former were yolk granules blackening with osmium tetroxide, while the latter consisted of rod-shaped mitochondria lined up perpendicular to the egg surface. The Golgi bodies, which were differentiated from the endoplasmic yolk by means of his methylene blue technique, were small endoplasmic spheres or vesicles. In the youngest cells the cytoplasm has a few chromophilic granules (? mitochondria) and groups of osmiophilic vesicles which separate when the oocyte is 15μ. The mitochondria assume a peripheral position when the oocyte is 25–30μ in diameter. There was evidence of clumping and formation of fat in the Golgi bodies as the egg developed. The cell on spawning was in the metaphase of the first reduction division.

Investigations prior to the advent of modern cytological methods were not abstracted. They are referred to by Wilson (1925). The papers of Coe (1930-47) on the histology of gametogenesis in various pelecypods will not be considered since the cytological aspects are not dealt with.

Roughley (1933) describes some histological aspects of oogenesis in the present species.

II. MATERIALS AND METHODS.

1. *Living Material.*

The oysters used in this investigation were obtained from the C.S.I.R. experimental lease at George's River and were 2-3 years old. The chlorinity of the water on the lease fluctuates slightly around 19‰ and only rarely falls below this figure. On receipt, the oysters, which had been out of water for 24–48 hours, were placed in a large glass trough of aerated oceanic sea water (Cl 19‰). They were usually kept in this trough until required and were never used unless they had been in it for at least an hour. As long as adequate aeration was maintained they remained satisfactory for use for

some weeks without food and without a change of water. However, fresh oysters were procured weekly. During the period of this investigation, most animals possessed ripe gametes, and this state appears to exist for about five months of the year (Kesteven, unpublished data).

The animal is opened and transferred to a dish of sea water. A sample of gonad contents is obtained by scraping a part of the ovarian wall onto a slide, and the sex determined by examination with low power. The visceral mass is separated from the surrounding tissues with fine scissors and given two more washes in fresh sea water. With a small ophthalmic scalpel the vesicular tissue covering is reflected and the tissue shaken in fresh sea water. Further fine dissection down to the brownish digestive diverticula, with intermittent shaking in sea water, removes most of the eggs in the ovary. From six medium sized oysters, 0·9 gm. of alcohol-ether dried eggs was obtained. Any large material may be removed by filtration through 80- and 200-mesh plankton netting—the eggs will pass new 200-mesh net without damage. For fertilization experiments, damaged eggs may be separated by allowing short periods of settling, followed by pouring or siphoning off the supernatant. The early oocytes may be concentrated by differential centrifugation.

The use of sea water as the suspension medium proved entirely satisfactory for oocytes of all stages. Monti has shown that in *O. edulis* and *M. edulis* the body fluids are isosmotic with sea water.

Eggs so removed from the ovary were considered essentially comparable with naturally spawned eggs for the following reasons: (*a*). No cytological or cytochemical differences existed between ovaries removed from animals known to be in the act of spawning and the ovaries of mature females used here. (*b*). No such differences existed between naturally spawned eggs and eggs artificially removed. (*c*). Eggs so removed could be fertilized and undergo normal development.

Special methods used in the study of living eggs are given in the text.

2. *Fixed Preparations.*

The following fixatives were used: Bouin, Helly (routine fixative) with or without post-chromation for 48 hours at 40°C. In 2·5% potassium dichromate, Champy (with 2·5% NaCl added for osmotic reasons), Aoyama and Baker's formol calcium (both with 1·5% NaCl added for osmotic reasons), chilled acetone, Mann's fixative followed by Ludford's modification of the Kopsch procedure and the Kolatchev method.

Dehydration was effected by alcohol, dioxan, acetone and by freezing drying. The latter, which was designed for the study of lipide cytochemistry, consisted of freezing a fixed block of tissue on a freezing microtome and transferring rapidly to a bottle containing silica gel (with indicator) kept in the freezing chamber of a refrigerator. The bottle is then rapidly evacuated with a Hyvac pump. To increase the rate of freezing and also to make the block more rapidly removable from the freezing microtome, small quantities of 40% alcohol were used. Too much alcohol is to be avoided because of the chance of contaminating the oil in the pump. After dehydration (24–36 hours), the block is removed and placed in a small specimen tube resting in a test-tube of paraffin in an embedding oven. After evacuation of the test-tube it is tilted and the paraffin allowed to permeate the block of tissue. This embedding process takes only a few minutes.

The following stains were used: iron haematoxylin, Ehrlich's haematoxylin, sudan black, Bensley-Cowdry, and Champy-Kull. The Feulgen method used was that of Rafalko (1946), since his reasoning seemed cogent and a more intense stain without any loss of specificity was achieved than with the older methods. Hydrolysis times were 8 minutes for Helly preparations, 25 minutes for Bouin.

The Masson technique proved very useful as a routine stain for this material and several other invertebrate tissues have also been successfully stained. The greater ease of histological analysis in specimens which show a good differentiation of structures makes the capriciousness of the method well worth bearing. The techniques described

for mammalian material were unsatisfactory, since the light green was invariably removed by the final aqueous acetic acid wash.

The following method was found satisfactory (after Helly fixation):

(a). Place in 5% ferric alum 5 minutes. (b). Wash rapidly in water. (c). Place in haematoxylin 5 minutes (2% solution of haematoxylin in 95% alcohol (ripened with hydrogen peroxide) 1 part, distilled water 4 parts). (d). Wash in water. (e). Stain 7 minutes in ponceau-acid fuchsin stain (ponceau 2 R 0·7 gm., acid fuchsin 0·3 gm., 1% acetic acid 100 ml.). (f). Wash in 1% acetic acid. (g). Place in phosphotungstic orange G solution 4 minutes (phosphotungstic acid 5 gm., orange G 1·5 gm., distilled water to 100 ml.). (h). Drain and place in light green solution 2 minutes (light green SF 2·5 gm., 2·5% acetic acid 100 ml.). (i). Drain, dehydrate rapidly in 95% alcohol and place in absolute alcohol. (j). Take each slide separately to a solution of 5% acetic acid in 95% alcohol and differentiate the green colour. (k). Pass through absolute alcohol, xylol, and then mount. Step (j) is the critical one, but the colour of a properly differentiated section is recognized with a little practice and the step is sufficiently slow to give an adequate margin of safety.

In Mann-Kopsch preparations the ground cytoplasm blackened to such an extent that the cytological structure was obscured. Reduction of the post-osmication to 24 hours did not obviate this, neither did turpentine remove the colour. It was found that potassium permanganate ($\frac{1}{2}$%) for $\frac{1}{4}-\frac{1}{2}$ a minute followed by oxalic acid (5%) for $\frac{1}{2}$ minute removed the extraneous colour completely. Leaving in permanganate for up to 8 minutes removed little more colour than a 12-second treatment and evidently only artefactory osmium blackening was removed. It is possible that some of the ground plasm reaction was due to the breakdown of some of the lipide granules, since not all the lipide bodies in any cell were perfectly fixed except in preparations made directly on the slide.

Centrifugal studies were made using an International S.B.I. centrifuge at a speed of 4,500 r.p.m. (approx. 3,500 g.) for 15–30 minutes.

Eggs removed from the animal, as described, were suspended in sea water and 5 volumes of 0·9 M (31%) sucrose added. This gave a flotation medium approximately isopycnotic with the eggs. After centrifugation the eggs were either studied fresh or fixed in 1% osmic acid or Helly's fluid. After fixation the centrifuged eggs were either embedded in paraffin or smears were made from the egg suspension.

Measurements were made by one of four methods: (a). For the smallest measurements, a Zeiss screw ocular-micrometer (1 division on drum = 0·1795μ); (b). by drawing with a *camera lucida* and measuring the drawing (1 mm. = 0·69μ); (c). by means of an ordinary graduated slip in the eyepiece (1 div. = 1·42μ); (d). for irregular objects by *camera lucida* drawings followed by measurement of the area with a planimeter; areas are then converted to the diameter of the circle with the same area (one planimeter unit = 15·8μ^2). All equivalents given are for 1/12″ objective and ×10 eyepiece. Method (c) was little used and was the least accurate for the sizes here measured.

The microscopical examinations were made on a Spencer research microscope fitted with the following apochromatic lenses: 8 mm., 4 mm. (NA 0·95) and 2 mm. (NA 1·3). An achromatic oil immersion condenser (NA 1·3) and critical illumination of the Koller type, using a 6-volt filament lamp and a Watson Conradi condenser made up the illuminating equipment. With this equipment the rows and dots on the diatom *Amphipleura lindheimerei* could be easily resolved with central illumination. Of the diatoms available this was the most difficult to resolve; it was from a Flatters and Garnett test plate of 15 forms. No loss of resolution occurred in photographs of the diatom at a magnification of 1,000 diameters (see Plate xvi, fig. 5).

III. The Anatomy and Histology of the Ovary.

The gonad in the mature animal lies at the apex of the visceral mass just inside the hinge. It covers most of the ventral surface, but dorsally is shorter, extending as far as the pericardial sac.

The ovarian tissue lies between the external vesicular tissue and the digestive diverticula, being separated from the latter by a variable layer of vesicular tissue. In the unripe ovary these vesicular tissue layers are quite well defined, but in the ripe animal are much reduced. Roughley (1933) has given a full description of the duct systems associated with the ovary.

The ovarian tissue itself is divided into lobules which, in the unripe ovary, are fairly widely separated by vesicular tissue. This, in the ripe state, is reduced to a few attenuated strands. Lying on this vesicular tissue basis are cell types A, B and C, and occasionally D, while the mature oocyte lies in the lumen. There is no stalk connecting these cells with the follicle wall as has been described for some other pelecypods.

The following cell types may be differentiated in Helly-fixed specimens. Most features are described from Masson or iron haematoxylin preparations. The measurements are from fixed preparations and are to be used in a relative sense.

1. Germ Cells.

Type A. The Definitive Auxocyte.

This appears in Helly- and Bouin-fixed specimens as a tightly entwined clump of chromosomes surrounded by a clear area. The cell is 4–5μ in diameter, the chromosome clump making up about two-thirds of this. The clear area cannot be stained, but appears to be surrounded by a very thin rim which presumably represents cytoplasm.

The cell was present in all ovaries examined from the wintering to the spawning state. It appeared to decrease in number as the ovary developed, but this may have been due to the general expansion of the follicle wall as it became distended with ripe eggs.

The cell is identified as a definitive auxocyte, i.e., an oocyte just before entry into the growth phase. Evidence supporting this contention is as follows: (a). The chromosome formation can be traced in a continuous series from this cell up to the chiasmata of the ripe egg. (b). The constancy of the cell throughout the whole of the time of ripening of the ovary, i.e., it is not a dividing cell. (c). Morphometrically the germinal vesicle (i.e., chromosomes and clear area) has a slightly smaller diameter than the next stage described and the nucleolus/germinal vesicle and germinal vesicle/cytoplasm growth graphs extrapolate (at zero nucleolus and zero cytoplasm, respectively) to a figure very near the diameter of this cell.

No nucleolus is visible in this cell (Pl. xvi, figs. 6, 7, 14).

Type B. Auxocyte 1.

This differs from the foregoing in possessing a well-defined area of cytoplasm surrounding a germinal vesicle in which the chromosomes have become more spread out and which possesses a nucleolus. The cytoplasm is often somewhat flattened along the follicle wall. The dimensions of the cell are: nucleolus 1·7μ, germinal vesicle 6μ, whole cell 9μ. Cells intermediate between A and B were found without a nucleolus and with reduced cytoplasm.

The cytoplasm is homogeneous, the germinal vesicle centrally placed and the nucleolus excentric, but not in contact with the membrane of the germinal vesicle (Pl. xvi, figs. 8, 14; Pl. xvii, figs. 26, 32).

Type C. Auxocyte 2.

This cell is larger than the foregoing and possesses P granules in the cytoplasm. Typical dimensions are: nucleolus 2·3μ, germinal vesicle 7μ, whole cell 12·6μ.

The chromosomes are more widely spaced and the excentricity of the nucleolus not so marked, possibly because of its larger relative size. The germinal vesicle is central and the cell usually spherical. The granules appear in a group at one pole of the nucleus and in the typical cell are about three in number. There is a tendency for patches of chromatin to adhere to the germinal vesicle membrane (Pl. xvi, figs. 8–10; Pl. xvii, figs. 27, 28, 30, 31; Pl. xviii, figs. 34, 38, 39).

Type D.   Auxocyte 8.

This is an oocyte which is about half grown. It is a spherical cell of diameter 20μ with a central germinal vesicle of diameter 11μ containing an excentric nucleolus 4·2μ in diameter. The cell is usually separated from the follicle wall, lying free in the lumen.

The P granules which have reached about their maximum number are found in groups of 10 or so and begin to show evidence of the peripheral location typical of the mature egg. The chromosomes are beginning to show the formation present in the mature oocyte (Pl. xvii, fig. 32; Pl. xviii, figs. 35, 37, 42).

Type E.   The Mature Oocyte.

The shape of this cell is often irregular in fixed preparations, due partly to shrinkage and partly to deformation by surrounding cells. The cell lies free in the lumen of the follicle. The nucleolus still lies peripherally in a spherical germinal vesicle which often contains small round particles ½–1μ in diameter. They are distinct from the nucleolar fragments sometimes found. The chromosomes can usually be seen near the germinal vesicle membrane as fine paired structures showing chiasmata.

Typical dimensions for this cell are: nucleolus 4·6μ, germinal vesicle 21μ, whole cell 38μ. The P granules have now adopted their typical cortical position and the broken down L granules can be seen in the medulla of the cell (Pl. xviii, fig. 45; Pl. xix, figs. 54, 55; Pl. xx, figs. 56–58, 60).

2. Non-Germinal Cells.

Type F.   The Wandering Tissue Cell.

This cell is widely distributed in the animal. In the ovary it occurs both in the vesicular tissue between the follicles and also sometimes in the follicle itself, especially in the earlier stages of ripening.

The nucleus, which has a diameter of about 3μ, is coarsely granular with a peripheral rim of chromatin under the nuclear membrane. It is spherical and usually centrally placed in the cell. The cytoplasm is usually hyaline but often appears somewhat vacuolated. The cell diameter is 5–6μ.

The granular cells of this type which have often been described in molluscs (see, e.g., Liebman, 1946) were not a feature in the present material (Pl. xvi, figs. 13, 15).

Type G.   The Fixed Vesicular Tissue Cell.

Usually no cytoplasm can be seen in this type. The nucleus is elongated and irregular in shape, lying along the main strands of vesicular tissue. Its size and chromatin distribution are essentially similar to the wandering tissue cell (Pl. xvi, figs. 9, 15).

3. Undetermined Cell Type.

Type H.

This cell occurs in the ovarian area between the follicles and also around the digestive apparatus. Its frequency is variable, but it appears to be commoner in mature ovaries.

The nucleus is somewhat larger than the above two cell types, ovoid (diameter 4μ), and its chromatin texture is looser. A very small nucleolus is present and usually no cytoplasm can be distinguished. The significance of this cell was not determined (Pl. xviii, figs. 35, 36).

It is not the purpose of this paper to consider germ cell cycles or sex change. It may be stated, however, that evidence, as sure as any evidence based entirely on fixed preparations can be, was found for the latter. It does not, however, appear to be a very common process and its recognition needs careful study with high powers of the microscope. Roughley (1933) has discussed aspects of the sex change in this species.

IV. SYSTEMATIC STUDY OF THE VARIOUS CELL STRUCTURES IN OOGENESIS.

1. *The Nucleus.*

(a). *The Nucleolus.*

The nucleolus first appears in the early growing oocyte. It is always spherical and probably always excentrically placed in the germinal vesicle. The excentricity, as far as can be judged, is not due to gravity. It has never been seen in contact with the germinal vesicle membrane and its position in the germinal vesicle does not change during yolk formation. It is well stained in iron haematoxylin preparations, is differentially stained yellow in Masson preparations when differentiation of the iron haematoxylin is carried far enough, and is brilliant red in Bensley-Cowdry preparations. The internal differentiation often found in solitary nucleoli in oogenesis is not found in stained or unstained preparations mounted in euparal at any stage. Unstained Helly preparations mounted in low refractive index media sometimes show the presence of refractile granules in the centre of the nucleolus in mature oocytes. These cannot be seen in the living egg.

Nucleolar fragments have been observed lying free in the nucleoplasm but not in contact with the germinal vesicle membrane. For the following reasons they are considered artefacts: (a). They are only occasionally observed. Their appearance is apparently a peculiarity of the individual, since other animals of the same batch similarly fixed and treated do not show it. (b). What are apparently stages in the formation of these fragments can be seen in occasional osmic-fixed whole egg preparations. There is first a dumb-bell appearance as if the nucleolus is herniating, and this gives rise to a dimorphic appearance—the parent body being well stained in the osmium and the derived satellite body (still in contact) having the appearance of a vesicle and causing little deposition of osmium. From this can apparently be formed vesicles (or rather smaller bodies having the appearance of the satellite) and also solid bodies, either by collapse of the vesicle or by further fragmentation of the parent body. Text-figure 1 illustrates the process. (c). Fragmentation could be regularly seen in acetone-fixed preparations while appearing rarely in ovaries fixed by other methods. (d). As described later in osmotic studies, an incipient fragmentation could be observed in the living egg. (e). Neither the fragments nor the nucleolar abnormalities can be seen in the normal living egg. (f). When present, the process is confined to mature eggs and is not found in immature oocytes.
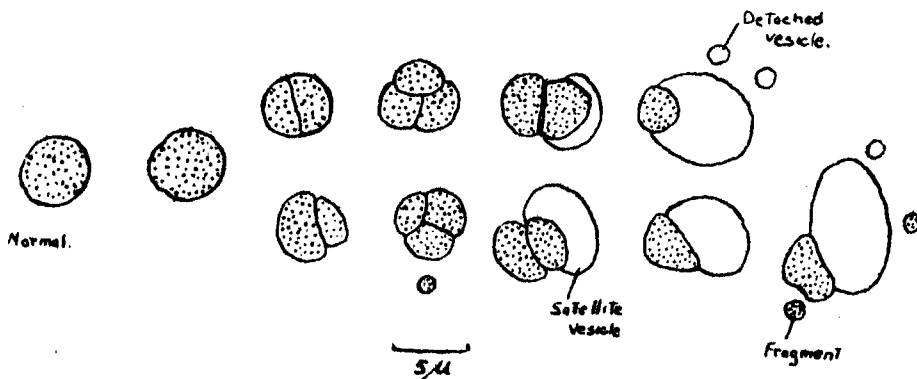
Text-fig. 1.—Formations interpreted as early stages in the formation of nucleolar fragments. *Camera lucida* drawings from whole eggs fixed in 1% osmium tetroxide. Compare with Plate xvii, figs. 10-19.

A very large body of literature exists concerning nucleolar extrusions in oogenesis, some of it not very critical. The extrusions are usually considered to be the precursor of protein yolk. That the process occurs in some forms is beyond all reasonable doubt, and it has been observed in the living egg (e.g., Duryee, 1941; Johnson, 1946).

Plate xvi, figures 11, 12, and Plate xvii, figures 16–19, 22, 24, illustrate these observations.

(b). The Chromosomes.

The chromosomes in the definitive auxocyte are fairly condensed, closely aggregated, fairly large structures showing no evidence of coiling. As the cell grows, the chromosomes do not grow in proportion and become more tenuous and diffusely scattered. There is little tendency to peripheral aggregation in auxocytes 1 and 2, although there is usually a Feulgen positive rim inside the germinal vesicle membrane. In auxocyte 3 there is a tendency to peripheral placing of the chromosomes, and in these cells the chromosomes stain less deeply in Feulgen than those preceding or following. In the mature oocyte the chromosomes are paired, thin, coiled structures in which chiasmata can be seen. These pairs are usually peripherally placed in the germinal vesicle but are not in contact with the membrane.

Bouin and Helly fixation both preserved the chromosomes well. The former often permitted a more intense Feulgen stain, but the latter showed more coiling and longer chromosomes, and was considered to give a better preservation. In Helly preparations the length of straight chromosomes was up to 12μ, and there was also a constant relation between a chromosome pair and the nucleolus. The maximum number of pairs observed was five.

In order to check the chromosome number, eggs were fertilized and allowed to develop to the 2–4 cell stage. The eggs were fixed in Bouin and sectioned and stained by the Feulgen procedure. The metaphase plates proved difficult for chromosome counts because of the small size of the chromosomes (1.5μ) and their close packing (metaphase polar diameter 4μ). Counts of 8–11 were encountered and 10 was the most common number. Chromosome morphology, meiotic divisions, etc., will be considered at a later stage in dealing with the early development of the fertilized egg.

No statements on chromosome number in oysters could be discovered in the literature. The only indication is a figure by Coe (1931) for spermatocyte divisions in *Ostrea lurida*, in which he figures 10 chromosome pairs. In the text, however, he states that chromosome counts were difficult to make "although the number is not large".

Plate xvi, figures 6, 9, 10, Plate xvii, figures 20–25, and Plate xix, figures 50–52, illustrate the chromosomes.

(c). The Karyolymph.

None of the fixatives employed preserved the natural homogeneous structure of the karyolymph in the mature or half grown oocyte, although earlier stages were well preserved by many. All caused varying amounts of vesiculation, giving a reticular appearance to the fixed germinal vesicle. This suggested that the contents had a high water content. This was borne out by the centrifugal experiments.

The reaction of the reticulum was amphophilic. Small, relatively basophilic granules were noticed in the germinal vesicle, but had no relation to the chromosomes nor did they appear to be nucleolar fragments (Pl. xx, fig. 60).

(d). The Nuclear Membrane.

The germinal vesicle membrane is quite distinct in iron haematoxylin preparations mounted in euparal. It occasionally shows wrinkles on its surface.

The membrane is more distinct in the early oocytes in iron haematoxylin preparations, but this was considered to be due to the presence of a chromatin rim (possibly extrachromosomal) just inside the membrane. The basophilia of the membrane itself shown in iron haematoxylin preparations, is less evident in toluidine blue or Ehrlich's haematoxylin preparations. Its thickness was estimated to be 0.3μ and no change in the thickness was evident during the growth of the oocyte.

(e). The Nucleolus-Germinal Vesicle Relation.

When the nucleolar diameter is plotted against the germinal vesicle diameter, an asymptotic type of curve results; the growth of the nucleolus, in effect, ceases when the

cell is half grown. This rapid growth phase covers the time in which the P granules are formed, and the cessation of growth of the nucleolus corresponds to the time when P granule formation seems complete. Text-figure 2 illustrates these data. The curve dotted in the middle of the main curve appeared to exist, but since it could not be correlated with any cytological observation, its statistical significance was not investigated. It will be seen that extrapolation to zero nucleolus corresponds fairly well to the diameter of the definitive auxocyte (cell type A).

(f). The Nuclear State on Spawning.

The oyster is of the *"Ascaris"* type (Wilson, 1925) or of class 1 of Just (1939) in that the germinal vesicle is intact on spawning and does not break down until fertilization occurs, when two reduction divisions occur rapidly. This condition on spawning appears to be common among pelecypods (Just, 1939; Wilson, 1925).

2. *The Cytoplasm.*

The Granular Categories.

Wherever feasible centrifugal stratification would seem to be the simplest, easiest and most accurate method for differentiating the granular categories in any cell. In the present material two clear-cut granular categories occur, which, because of their cytochemical reactions, are termed P and L granules (protein and lipide, respectively).

(a). The P Granules.

These granules are visible in living and fixed eggs as a cortical layer of granules which are smaller than the endoplasmic granules. They stain red in the Masson procedure and can be stained by iron haematoxylin, but usually the L. granules, either whole or broken down, mask the distribution of these bodies since the L granules also stain. The clearest differentiation is seen in Bensley-Cowdry staining after Helly fixation and in the Champy-Kull procedure. Their integrity and cortical position are preserved after Champy, Helly, Mann and acetone fixation, but are evidently not preserved after Bouin or Baker fixation.

They first became evident as a small group of three or so in the cytoplasm of cell type C rather nearer the nuclear membrane than the cell membrane. A careful study of the germinal vesicle membrane at this stage shows the presence of fuchsinophilic granules attached to its outer surface which were at first thought to represent either the point of origin of the granules themselves or of their presubstance. The attached granules are not present in cells before the origin of the P granules and are not seen in cells in which the granules are numerous (before auxocyte 3). There was no concentration of the granules beneath the P granule group and they occurred more or less evenly distributed around the membrane. As will be shown later, these granules are artefacts, representing disintegrated L granules which have become adherent to the nuclear membrane.

The orientation of the P granule group was tested against the position of the nucleolus and the position of the follicle wall. The former showed no constant position in relation to the granules. The granules, however, showed a constant orientation to the follicle wall, appearing in that part of the cell which is furthest from the wall. In a few cases this could be ascribed to the proximity of the germinal vesicle to the follicle wall, thus leaving insufficient cytoplasm on the proximal side of the cell to contain any granules. However, in the majority of cases such an explanation was not tenable.

The granules increase in number possibly partly by new formation and partly by division of pre-existing ones, since they tend to occur in groups of 10 or so. No perinuclear concentration was observed at any stage, and there seems to be a random migration to give a more or less even cytoplasmic distribution. Auxocyte 3 shows some evidence of the cortical movement and often the grouping noted above can still be seen.

The mature egg shows fairly complete restriction of the granules to the cortex. Some appear to occur in the medullary region, but most of these are probably broken down L granules, which have similar staining properties.

There is a small increase in diameter of the granules during oogenesis. In the mature egg the granules are invariably spherical and measure about 0·5μ in diameter.

Plate xvii, figures 26–32, Plate xviii, figures 33–37, and Plate xx, figure 60, illustrate the P granule formation.

(b). The L Granules.

The L granules are not well preserved in Helly, Baker or Bouin fixatives although much of their lipide content is retained. They are preserved in Champy, to a variable extent in Aoyama, and usually in post-chromated Helly preparations at least in small pieces of ovary. Mann-Kopsch preparations gave the best demonstration, although even here the preservation was never perfect, there still being some tendency for coalescence of the granules—a situation never seen in the normal living egg. Their diameter in such preparations varied between 0·7μ and 1μ.
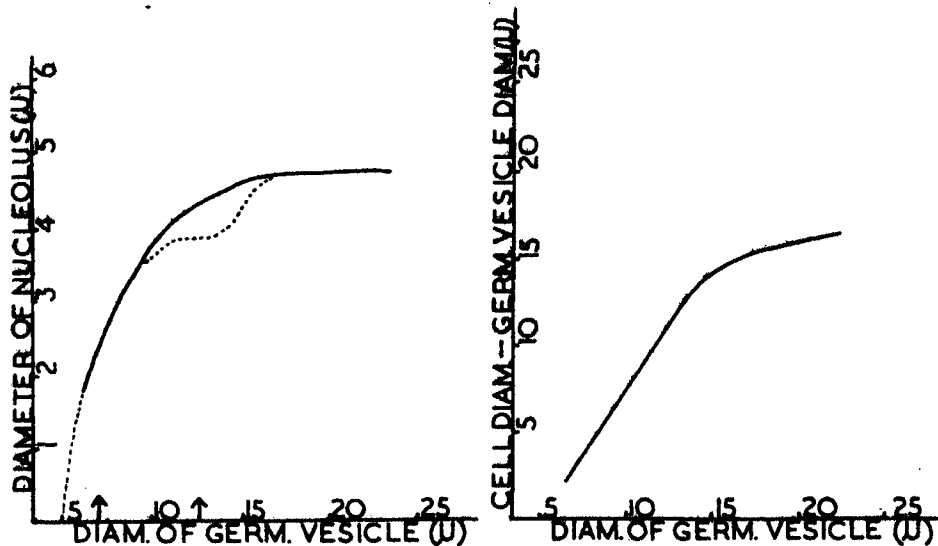
Text-figs. 2–3.—Illustrating the relation between nucleolus and germinal vesicle diameters (Text-fig. 2) and germinal vesicle and cytoplasm diameters (Text-fig. 3). The arrows show the beginning and end of P granule formation.

They arise first in a cell about the same size as that in which the P granules first appear (cell diameter 12·5μ, germinal vesicle diameter 7·4μ). The granules are somewhat smaller than those in mature eggs and arise randomly in the cytoplasm. While groups may be present at one pole of the nucleus, this is not typical enough to be generalized. There is a slight tendency to grouping of the granules, and no orientation in respect to germinal vesicle, L granules or follicle wall could be seen.

The granules increase both in number and size as the oocyte becomes more mature. The increase appears to be continuous and without break.

That there has been no confusion of L and P granules in the early stages is evident from their different behaviour. Furthermore, they may be demonstrated together fairly satisfactorily in Mann-Kopsch slides by permanganate bleaching followed by an hour or more in 4% chromic acid and then staining by the Altmann method. The same simultaneous demonstration can be seen in Champy-Kull preparations.

Plate xviii, figures 38–45, Plate xix, figures 46–49, 54, 55, and Plate xx, figures 56–59, illustrate the L granules.

(c). The Ground Plasm.

The ground plasm appeared homogeneous, and no granules could be detected in it by any technique.

(a). *The Cell Membranes*.

As will be seen later, there are probably two membranes present: a plasma membrane and an external membrane. The latter, due to its lack of staining, and despite its considerable thickness, does not usually show in sectioned material mounted in euparal. When cut tangentially there is some evidence of it, on careful focussing, but it is not visible in radial section. When the refractive index of the mounting medium is lowered (e.g., in aqueous mounting medium for sudan black preparations), or in sections not completely dehydrated before mounting, it appears as a refractile body.

The plasma membrane cannot be seen at any stage.

(e). *The Germinal Vesicle–Cytoplasm Relation*.

Text-figure 3 indicates that there is a linear relation between germinal vesicle and cytoplasm diameters for most of the growth period, but the germinal vesicle appears to continue to grow after the cytoplasm has reached its maximum size. However, when the volume of the nucleus is plotted against the volume of the cytoplasm, a linear relation is found. It will be seen that extrapolation to zero cytoplasm gives a value agreeing fairly well with the diameter of cell type A.

V. OBSERVATIONS ON THE LIVING EGG.

Mature eggs separated from the ovary and examined in sea water are usually spherical bodies about 50μ in diameter. No accurate measurements of the living egg were made. There is no pigment visible nor can any be extracted with lipide solvents.

The germinal vesicle is optically homogeneous and the nucleolus can be made out as a slightly refractile body placed excentrically in the germinal vesicle. It shows no structure and in undamaged eggs is perfectly spherical. No trace of the chromosomes can be found in living eggs, nor are any granules visible in the karyolymph.

The cytoplasm is filled with refractile granules, closely packed. Careful examination reveals a cortical layer, a few granules thick, in which granules smaller than the medullary granules occur. No brownian movement is visible in normal eggs nor is there any cytoplasmic streaming, but in injured eggs brownian movement occurs.

Young oocytes were gathered by differential centrifugation. An ovarian suspension was first centrifuged at 400 g. for 3 minutes. This removes mature oocytes, large ovarian debris, etc. A further centrifugation of the supernatant at 3,000 g. for 5 minutes concentrates the young oocytes. These were suspended in a few drops of sea water and examined. In the youngest oocytes (type A) no cytoplasm could be distinguished nor could the chromosomes be seen. In cell type B the cytoplasm was homogeneous and in the germinal vesicle no chromosomes nor nucleolus could be seen. The invisibility of the nucleolus is not unexpected, since the much larger nucleolus of the mature eggs usually requires a careful search before it is found. Cell type C showed the presence of highly refractile granules in its cytoplasm (from one to several), but again the nucleolus was not visible. By their number and grouping these granules were considered to be P granules. At the time of these observations the early cytology of the L granules had not been worked out and these were not looked for specifically. However, it would appear that they are not visible at this stage. Cell type D had the same structure as the fixed preparations indicated. No brownian movement occurs in these young oocytes.

Various abnormalities of mature oocytes, collected by the method described, were noted. They were due to the processes involved in making an egg suspension, but are of interest in showing the structure of the egg. (a). Retraction of the cytoplasm from the external membrane. This was fairly common but no special treatment was found to influence its occurrence. It is definitely not a plasmolytic phenomenon; it had no relation to the osmotic pressure of the suspension medium. The germinal vesicle was not visible in these eggs, but whether or not its breakdown was the cause of the cytoplasmic contraction cannot be stated, since, in any case, the close packing of the granules would prevent the germinal vesicle from being seen. The space so formed is

clear and free from granules. It is definitely not due to a lifting off of the external membrane. (b). A crenated appearance was sometimes found in concentrated egg suspensions which had been left for some time. It usually disappeared when the suspension was shaken or diluted. It was thought that anaerobic conditions had something to do with its appearance. (c). Projections from the external refractile membrane at one or more points along its surface. This was not very common and was considered to be due to mechanical injury of the membrane itself. It was not a myelin formation. The rest of the cell preserved its normal morphology. (d). Presence of brownian movement was considered evidence of the moribundity of the cell. (e). Abnormalities of the shape of the nucleolus were often associated with abnormality (d). (f). Aggregation of granules (L granules) in the cell was also considered to be an indication of moribundity. (g). In cells which had been completely cytolysed, the germinal vesicle and outer cytoplasmic membrane could be seen as refractile bodies which preserved their usual form and relation to one another, but were smaller than in the living egg. (h). In some cells vesicular projections from the germinal vesicle were seen. They may be single or multiple and are usually connected with the germinal vesicle by a stalk, but may become separate to lie free in the cytoplasm. In centrifuged eggs these vesicles were the lightest bodies in the cell and tended to be extruded from the cell under the action of centrifugal force. They appear to be formed under pressure of the cover-glass and contain karyolymph.

When the cell membranes are punctured the granules flow freely out. The P granules appear to retain their identity and the L granules aggregate into irregular clumps. During this process of flowing out of the cytoplasm, the cytoplasm away from the break preserves its normal contours as it separates from the external membrane. That this is due to the presence of another membrane is evident from the rare cases in which this also shows a break in continuity, giving rise to an appearance illustrated in Text-figure 4. This latter membrane evidently represents the true plasma membrane, while that which has been referred to as the external membrane is probably a vitelline membrane.
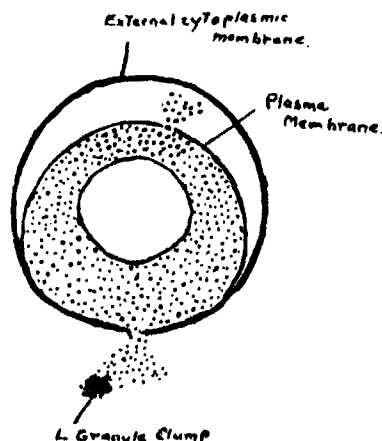
Text-fig. 4.—Showing the presence of two egg membranes in an egg which showed a simultaneous rupture in both.

The cells were examined under a polarizing microscope. The only machine available was a petrological microscope which was not very suitable for the high resolutions needed for small eggs. No birefringence was noted in these cells when mounted in sea water.

Due to the light scattered from the granules, dark ground examination did not reveal the cell structure as well as bright field.

1. *Effect of Osmotic Pressure.*

Sea water was concentrated by evaporation, aerated and the pH readjusted to 8·2. After dilution and addition of the egg suspension, the concentrations used were: 180, 150, 115, 100, 84, 50% of the original sea water. The eggs were examined after one hour. No serious attempt was made accurately to measure cell diameters, but subjectively there was little change. No change in granule integrity was noted at any concentration but there was an increase in the percentage of crenated cells in the higher concentrations. An incipient nucleolar fragmentation was observed after two hours in 50% sea water.

2. *Effect of pH.*

Sea water was adjusted to various pH's with acetic acid and sodium hydroxide. Eggs were left one hour before examination. At pH 2·6 the eggs were reduced in volume and appeared "fixed"; at pH 5·0 they were normal in every respect. Nucleolar fragmentation was observed in some cells at pH 9·5, but most were normal. Most eggs were cytolysed at pH 11·5, but those which preserved their integrity appeared essentially normal. The lipide granules are evidently either more stable to pH changes than those of the Amphibia studied by Holtfreter (1946a) or the egg is less permeable.

3. *Effect of Vital Dyes.*

By dilution of a 0·1% solution in distilled water with sea water, 0·0001% and 0·00005% solutions of the following dyes were prepared: neutral red "vital" (Gurr), janus green B (Grubler), brilliant cresyl blue (Gurr), nile blue (Grubler) and methyl green (Gurr); the latter because of its specificity for mitochondria in *Arbacia* eggs (Harvey, 1941). Methylene blue, 0·00002%, was used because of its alleged specificity for Golgi apparatus (Worley, 1943 *et seq.*). The eggs were examined at ½, 1, 3 and 24 hours.

With the exception of nile blue, none of the dyes stained the egg. After three hours in cresyl blue the eggs were macroscopically violet but this could not be seen microscopically. Neutral red sometimes stained a patch of granules opposite a visible abnormality in the external membrane, but normal cells never stained. Nile blue stained rapidly and, while no cortical differentiation was evident, by centrifugation of the eggs the stain was shown to be confined to the P granules.

In the same suspensions, inclusions in the ciliated gill epithelial cells, which were sometimes present, were found to stain with the dyes in the concentrations used.

In early oocytes, collected by differential centrifugation, the P granules stained with neutral red and methylene blue—the only dyes used on these cells.

Whether this lack of staining of mature eggs was due to non-penetration of the dye or to rapid reduction to a leuco form, was not ascertained.

4. *Effect of Centrifugation.*

Centrifugation of mature egg suspensions by the method described gave clear separation of the granules. Some batches of eggs were refractory. The centrifugal and centripetal poles could not be determined directly but were deduced from the following: (a). L granules are shown later to contain much lipide and may reasonably be expected to have a lower specific gravity than the cytoplasm. (b). P granules are shown to be composed of protein and may be supposed to have a higher specific gravity than the ground cytoplasm. Having determined which granule group is which, by cytochemical means, the poles may be identified in any cell by the position of the germinal vesicle and nucleolus: the former migrates centripetally and the latter migrates centrifugally in the germinal vesicle. The difference in specific gravity between the L granules and the germinal vesicle is evidently not very great because the former are packed around the centripetal circumference of the germinal vesicle. This confirms deductions, made in an earlier section, about the high water content of the germinal vesicle and also suggests that the specific gravity of the L granules approximates that of water. The lack of deformation of the germinal vesicle membrane by the nucleolus suggests that the latter has a specific gravity the same or less than the cytoplasm.

In dividing cells the centrifugal force used caused no change in position of metaphase or anaphase configurations. The cytoplasmic components of cells in mitosis were more difficult to stratify than those of resting cells.

One hour after centrifugation the granules in most oocytes were still stratified.

Plate xix, figures 50–53, and Plate xx, figures 61–64, show the formations observed in centrifuged eggs,

5. *Oxygen Uptake.*

In order to determine whether the eggs respired rapidly enough to be suitable for manometric studies, the oxygen uptake of fertilized and unfertilized eggs was determined by the direct method of Warburg. At 26°C. the Q_{O_2} (N) of unfertilized eggs was $-4·5$ and for fertilized $(2 \rightarrow 16$ cell) -14. Normal cleavage occurred in the flasks when shaken at 100 cycles per minute. The figure of Humphrey (1946) for adductor muscle of this species recalculated as Q_{O_2} (N) is -1 (at 26°C.). Warburg (1915) records values of $-1·5$ and -12 for unfertilized and fertilized *Strongylocentrotus* eggs of a comparable stage of development (at 23°C.). Whitaker (1931) finds a decrease of 45% on fertilization in *Cumingia* eggs. His values cannot be converted into Q_{O_2} (N).

VI. CYTOCHEMISTRY.

1. *Lipide.*

Variable amounts of sudan black stainable lipide were preserved by all the fixatives used. The following descending series was found: Helly with post-chromation, Helly, Baker and Bouin. The following descending series was found for the various dehydration techniques: freezing drying, dioxan and alcohol-xylol. As far as can be judged, the osmic-containing fixatives preserved the most lipide, but Mann-Kopsch did not appear to be very much better than post-chromated Helly. Unhydrolyzed Feulgen preparations of the sublimate containing Helly showed the same gradations in the dehydration series; the strongest reaction occurred in post-chromated Helly preparations.

Once fixed in Helly's fluid, the lipides are almost impossible to remove by extraction procedures, being more difficult to remove than was the case in snail spermatocyte dictyosomes studied by Baker (1944). All extractions were carried out in the Soxhlet apparatus at a temperature slightly less than the boiling-point of the extractant. After extraction, slides were stained in sudan black. Table 1 describes these data. The

TABLE 1.

Extractant.					Temperature.	Hours Extraction.	Degree of Extraction.
Alcohol-chloroform, 3 : 1	..	,,			75° C.	½	0·5
,,	,,	,,	..	..	,,	36	2·5
Do. permanganate*		..	...,		,,	½	2
,,	,,	..	..	..	,,	36	3
Ether	..	..	..	,,	37° C.	36	2·5
Pyridine	..	..	..	..	100° C.	36	3
,,	..	..	..	..	,,	72	4
Do. Permanganate*	..	..	..	,,	36	4–5
Xylene-acetic, 3 : 1	..	..	..	110° C.	½	8
,,	,,	,,	..	..	,,	1	9·5

* Indicates treatment in ½% KMnO₄ for two minutes followed by oxalic acid before extraction commenced.

figures showing the degree of extraction are approximate, 10 representing complete extraction. Frozen dried paraffin sections were used throughout.

Iron haematoxylin and unhydrolyzed Feulgen preparations of the extracted slides showed the same sequences as did sudan black. With the exception of xylene-acetic, extraction caused little or no change in the cytological details. After xylene-acetic extraction the cytological detail was obscured, evidently by solution of part of the protein. This probably allowed a more intimate contact between extractant and lipide.

Acetone-fixed paraffin sections were found to contain little or no lipide. The extraction presumably occurred mainly in the alcohol and xylol used both before embedding and also in bringing the sections on the slide down to water. Fixation in acetone or alcohol appears to be the only way of obtaining a lipide-free section—a matter of importance in glycogen cytochemistry.

Mann-Kopsch preparations, treated with permanganate for short periods in order to clear them, could be bleached to a considerable extent in turpentine. The osmic blackening was just visibly reduced in half an hour and was almost completely absent after four hours. At no stage of this extraction was any vesicular (rim) structure demonstrated in the L granules. Slides treated in turpentine for varying periods were stained in sudan black. After two hours' extraction, the morphological integrity of the L granules had been largely destroyed, and, presumably by migration of lipide, the cell cortex was no longer sharply differentiated from the medulla. However, there was still a considerable amount of lipide, demonstrable by sudan black, after four days' extraction in turpentine. Sudan black could be rapidly and completely removed from Helly preparations by treatment with absolute alcohol, but in turpentine-treated Mann-Kopsch preparations the time was much prolonged; evidently osmic fixation alters the sudan black solubility properties of the lipides in some way or preserves a further lipide class in which sudan black is very soluble.

Treatment of Helly preparations for two hours with turpentine caused no demonstrable decrease in the amount of sudan black stainable lipide.

The Aoyama method did not preserve the L granules very well, but in lightly impregnated preparations a blackened rim could be seen in the intact granules. This can hardly be interpreted as an indication of a core of neutral fat, since the impregnation seems to be due to a deposition of finely divided metal produced outside the structure impregnated. The rim would be due to the fact that the silver had not yet penetrated into the core of the granule; sudan black staining of Aoyama preparations indicates that this is the case. More deeply impregnated Aoyama preparations show the L granules as solid, but whether this is due to penetration of the silver particles into the centre, or merely to a cortex so dense as to obscure any internal differentiation, cannot be decided.

The identity of the lipide classes—phospholipide, fatty acid and neutral fat—is difficult to recognize cytochemically when the three are present together. Because of

TABLE 2.

Hours Extraction.	Degree of Extraction.	Appearance.
0*	—	Lightly stained globules.
1	0	Intensely stained rims, no centre.
6	2·5	,, ,, ,, ,, ,,
12	5	,, ,, ,, ,, ,,
24	8	Lightly stained rims.
36	10 (complete)	—

* Taken up to xylol and down again to water.

the solubility properties of the fixed lipide in the present material, the presence of phospholipide seems proved. Helly-fixed free fatty acid will resist extraction for a considerable time. Oleic acid was emulsified with gelatine and smeared on slides. After fixation in Helly they were subjected to varying times of extraction with alcohol-chloroform mixture and stained in sudan black, giving results which are set out in Table 2 (cf., Tennent and Gardiner, 1930).

It is evident from the above that the L granules cannot be composed entirely of fatty acid, but it cannot be decided whether fatty acid is present or absent in them.

Nor is the presence or absence of neutral fat easy to determine. The previous observations suggested that it was not present, but neutral fat may have been extracted before the slides reached the sudan black (i.e., during embedding, and in bringing the slides to water). As sudan black staining is really too intense to enable small changes in lipide concentration to be observed under the microscope, the sudan IV method of Kay and Whitehead (1935) was used on isolated eggs. Individual L granules were studied as far as possible and estimated degrees of staining found are set out in Table 3.

TABLE 3.

Material.	Degree of Staining.	Remarks.
Fresh egg*	10	Granules mostly coalesce.
Acetone-fixed egg	6	„ „ „
Helly-fixed egg	10	Granules mainly intact.
„ „ „ acetone treated	8	Granules largely coalesced.
„ „ „ alcohol treated	7	„ „ „
Paraffin sections (frozen dried)	6	„ „ „

* Gave clear demarcation between cell cortex and medulla.

The above was considered to indicate the probable presence of neutral fat although the amount is not necessarily in relation to the degree of reduction of staining noted above. Little difference in size of the L granules in living, Mann-Kopsch or post-chromated Helly-fixed eggs could be seen, although such a difference might be expected if neutral fat were dissolved out of the granules.

The cytochemical evidence thus points to the presence of phospholipide, neutral fat and possibly free fatty acid, in the L granules.

In the mature egg cytoplasm, lipide is confined to the medullary region; no lipide is present in the cortical P granules. In Helly, Baker and Bouin preparations, the breakdown of the L granules—followed presumably by some migration of lipide—obscures the lipide-free cortex to a variable extent. As far as can be seen, in preparations in which L granule morphology is completely preserved, no lipide occurs in the ground cytoplasm, but there is a slight sudan black staining of the L granule free cytoplasm of auxocyte 1. There is very light staining of the nucleolus and nuclear reticulum (cf., Stoneberg, 1939) and no apparent change in this staining is evident during the growth of the oocyte. An apparent light staining of the external cytoplasmic and germinal vesicle membranes was evidently an artefact, due to increased refractility in the water-mounting medium (low refractive index), since it was also evident in unstained preparations.

The fuchsinophilic granules on the germinal vesicle membrane, noted in a previous section, were considered artefacts due to adherence of broken down L granules to the membrane for the following reasons: (a). Similar formations could be stained by sudan black in the same cell types, but not in cell types other than those in which the

fuchsinophilic granules occurred. (*b*). They are not shown in Mann-Kopsch, Champy or Kolatchev in which the L granules are more completely preserved. (*c*). In post-chromated Helly preparations the same adherence to the nuclear membrane occurs in the early cells, but here the clumps are larger. (*d*). In cells where the formation is present, no L granules can be demonstrated in the cytoplasm; L granules are known to occur in the cytoplasm of cells of this stage in Mann-Kopsch preparations.

No attempt was made to follow sterol distribution.

Plate xix, figures 47–49, 53–55, and Plate xx, figures 58, 59, 61, illustrate some of these observations.

2. *Glycogen.*

The Bauer method, as described by Bensley (1939), was used, the Feulgen reagent and wash waters being those of Rafalko (1946). Chilled acetone was used as the fixative since with all other fixatives interference by lipide would be expected (cf., Holtfreter, 1946*b*). Most of the slides were lipide free to the sudan black stain but were given four hours' extraction with alcohol-ether (2:1) mixture first. This caused a slight reduction in the colour of the experimental slides in some cases, presumably due to removal of the small amount of residual lipide. Table 4 illustrates the results.

TABLE 4.

Slide.	Pretreatment.*	Colour.
1	None.	10
2	Distilled water 1 hr.	9–10
3	2% malt extract (40° C.) 1 hr.	7
4	Saliva (40° C.) 1 hr.	7
5	Saliva (40° C.) 4 hrs.	3
6	Straight into Feulgen.	0–1

* All slides placed into chromic acid and Feulgen reagent at the same time.

The residual colour in Slide 5 may be due either to incomplete removal of glycogen by salivary amylase or to the presence of another polysaccharide, e.g., galactogen which would not be attacked by the enzyme.

Little change in glycogen content could be seen during the growth of the oocyte. The reaction is confined to the cytoplasm.

3. *Alkaline Glycerophosphatase.*

The method of Gomori (1941) was used; a mixture of *a* and *β* glycerophosphates was the only substrate used. Slides of acetone-fixed ovary were incubated for 4, 8 and 24 hours at 40°C.; the high temperature did not inactivate the enzyme in the times used. A strong reaction was given by the digestive diverticula. The oocytes appeared to give a strong reaction, especially in the germinal vesicle on nucleolar fragments and other granules, but the same pseudo-reaction was present in slides incubated without substrate. Placing the slide in boiling water abolished the reaction in the digestive diverticula, but had no effect on the oocyte pseudo-reaction.

Phosphatase has been described in nuclei by most workers using the reaction—an observation substantiated by chemical evidence in the case of isolated liver nuclei by Dounce (1943)—and has been stated to be present on chromosomes by Willmer (1942), Krugelis (1941) and Danielli and Catcheside (1945). No such distribution either in chromosomes or nuclei could be demonstrated in the germinal cells of the present material.

N

4. *Protein.*

The Millon reaction was performed using the reagent of Bensley and Gersh (1933) and the reagent of Cole (1933) diluted 1:1. Attempts to use the Folin and Ciocalteau reagent were unsuccessful.

The Sakaguchi reaction was performed by the method of Thomas (1946). The staining was more intense than after Serra's (1946) method.

The distribution of fixed – SH groups was investigated on fixed material by the method of Serra (1946) before and after HCN pretreatment, and by the method of Brachet (1938) using separated mature eggs. Neither method gave rise to any colour, macroscopic or microscopic.

Bouin, acetone and Helly preparations were used.

Tyrosine.—Oocytes and digestive apparatus gave about the same colour. The vesicular tissue gave the least reaction, but it was proportionately more than for the arginine reaction. In the mature oocyte the nucleolar reaction was approximately the same as the cytoplasmic reaction. There was some increase in cytoplasmic reaction as the cell became more mature. In young cells the nucleolus gave a lighter reaction than the cytoplasm of its cell but this can be explained by the smaller size of the nucleolus in these cells (nucleolar diameter 2–4μ, section thickness 5μ). No difference in colour between P granules and ground cytoplasm could be seen.

Arginine.—Little or no reaction occurred in the vesicular tissue; the vesicular tissue nuclei were slightly differentiated. The oocytes gave a more intense reaction than the digestive apparatus (except for certain granules and the ciliary insertion regions). In the mature oocyte the nucleolus and cytoplasm gave about the same colour. Little change in apparent content was noted during the formation of the egg. No difference in arginine content between P granules and ground cytoplasm was found. The chromosomes of the definitive auxocyte were not well differentiated and the nucleus in the cells of the digestive apparatus was not differentiated from the cytoplasm. The fact that the nucleolus in the young oocytes gives about the same colour as the nucleolus of the mature egg, can probably be interpreted as meaning that the arginine content of the former is higher.

5. *Ribose Nucleic Acid.*

Attempts were made to demonstrate ribose nucleic acid by the McRary and Slattery (1945) reagent and by the methods of Mitchell (1943), but were not successful. Reliance had therefore to be placed in the distribution of basophilia. It was not convenient to prepare ribonuclease but the relative distribution of the basophilia, taken in conjunction with the analytical figures for ribonucleic acid, was considered to give a reasonably accurate relative idea of the distribution of the nucleic acid.

Toluidine blue and Ehrlich's haematoxylin staining of Helly, post-chromated Helly, Bouin- and acetone-fixed slides form the basis of the description. Acetone fixation, while probably satisfactory for histochemical comparisons, was not suitable for cytochemical *observations.* Helly and post-chromated Helly preparations gave essentially the same picture as Bouin, except that the degree of basophilia was reduced in all structures in the former fixatives. Ehrlich's haematoxylin gave essentially the same picture as toluidine blue.

Little change in nucleolar basophily could be seen as the cell developed, but there appeared to be some increase in the cytoplasm. The germinal vesicle membrane was usually well differentiated, but there was no staining of the external cytoplasmic membrane. A clear demarcation of the cell cortex was usually present—it was very lightly stained as contrasted with the deeply stained medulla.

Some of the medullary reaction was due to the presence of lipide, since the lipide granule debris attached to the nuclear membrane in the early cells was often differentiated from the cytoplasm. However, in Bouin preparations, the lipide-free cortex is seldom visible in sudan black preparations, while in the basophilia preparations the cortex was usually visible as a rim staining much less intensely than the medulla. The conclusion that the P granules contain little or no nucleic acid, and that the latter

is confined to the ground cytoplasm, seemed warranted. The fact that the nucleolar reactions of the early and mature oocyte are the same probably means that the nucleolus of the young oocyte contains more nucleic acid.

Harvey and Lavin (1944), on the basis of ultraviolet light photography, describe a maximum nucleic acid absorption in the clear area (ground cytoplasm) of the centrifuged *Arbacia punctulata* egg.

VII. CHEMICAL ANALYSES.

The figures here quoted are from analyses of a batch of eggs collected in March from seven oysters. This can hardly be considered representative of the population, but the results are reported primarily as a check on the cytochemical findings.

The eggs were removed from the ovary, centrifuged and dried by several suspensions in absolute alcohol over a period of two hours, followed by ether, and finally filtered on a sintered glass filter. The alcohol-ether drying fluids were combined and the volume noted. The weight of the dried egg powder was 980 mgm. and it was practically lipide free.

Stannous chloride was used for reduction of the phosphomolybdate complex, since it allowed the estimation of much smaller quantities of phosphate than other reducing agents. Deviation from Beer's law is corrected by a standard graph. Ribose nucleic acid (or more accurately residual pentose) was determined by a method similar to that of Davidson and Waymouth (1944). The pentose colour was developed in the NaCl extracts by the reagent of McRary and Slattery (1945) using xylose as standard. Glycogen was estimated by the method of Humphrey (1940b) for digestion, precipitation and hydrolysis, the reducing sugar being estimated by the method of Nelson (1944). Nitrogen was determined by direct nesslerization. Turbidities occurred in some estimations due to the large quantities of calcium and phosphate. They were overcome (a) by centrifugation if turbidity was slight; (b) alkalinization of digest and allowing calcium phosphate to settle; and (c) by Parnas–Wagner distillation and nesslerization of the distillate. Any turbidity in phosphorus determinations was removed by extraction of the molybdenum blue in butyl alcohol.

All figures quoted are means of at least one set of duplicates.

1. The Egg Powder.

The egg powder (11·7% total N, 1·31% total P) was subjected to the fractionation procedure of Berenblum Chain and Heatley (1939). The results obtained are set out in Table 5.

TABLE 5.

	Lipide Extract. (Alcohol, Chloroform, Ether.)	Acid Extract. (N/10 HCl.)	Residual Powder.
Ammonia N	—	Nil	..
Total N	0·135%	0·99%	10·2%
Total P	0·033%	0·56%	0·71%
Inorg. P (apparent)	—	0·14%	—
Organic P	—	0·418%	—
$\frac{N}{P}$	4·05	—	14·2

The residual pentose content of another sample of lipide and acid-extracted powder was found to be 2·7%. This powder was found to contain 1·15% phosphorus, so that in terms of the original unextracted powder, the pentose content is 1·66%. This

corresponds to a ribose nucleic acid content of 7·0% and to a ribose nucleic acid phosphorus of 0·67%. The closeness of this figure to that for residual phosphorus may be more apparent than real, since the method is subject to more error than most other estimations and needs careful checking in unknown material. The figures are much higher than those of Brachet (1931, 1936) for sea urchin eggs and those of van der Ghinst (1934) for trout eggs.

Glycogen was found to comprise 2·7% of the dried powder. This is considerably less than the glycogen content of dried whole oyster (Humphrey, 1941a), but may explain the seasonal curve of glycogen content which he found.

2. *The Drying Fluid.*

This contained 0·24 mgm. N and 0·105 mgm. P per 5 ml. A maximum of 0·08 mgm. of the phosphorus was soluble in hydrous ether and the nitrogen content could be reduced to 0·068 mgm. by leaving in contact with N/10 HCl overnight. It is evident that the N/P ratios have little significance.

An aliquot (45 ml.) of the drying fluid was evaporated under reduced pressure and the residue extracted with acetone. The acetone extract was centrifuged, evaporated and dissolved in alcohol. Titration of the alcoholic solution suggested the presence of free fatty acid equivalent to 0·67 ml. 0·04N NaOH. After saponification, this solution contained fatty acid equivalent to 0·6 ml. 0·5N NaOH. In order to eliminate water-soluble fatty acids, and because the titration had not been done on a microburette, the fatty acids produced by saponification were collected, washed, dissolved in alcohol, and titrated with 0·1N NaOH. They were equivalent to 2·43 ml. This figure was used for calculation. The acetone-insoluble fraction of the original fluid contained only 55% of the phosphorus present in the original drying fluid; this meant that the total fatty acid after saponification had to be reduced by an amount equal to the phosphatide present in the acetone extract (45% of whole phosphatide). It also meant that the apparent free fatty acid content was too high.

Calculation on the following bases: Phospholipide containing 3·8% P and 95% of total P in drying fluid being phosphatide P; phosphatide saponification number 130, neutral fat and fatty acid saponification number 190—suggested the following amounts of lipide in the drying fluid and calculated dry weight of lipide containing eggs. The figures are, of course, to be regarded only as approximations (see Table 6).

TABLE 6.

	Phospholipide.	Free Fatty Acid.	Neutral Fat.	Total.
Drying fluid	120 mgm.	<39 mgm.	306 mgm.	465 mgm.
Original dry weight	8·9%	<2·7%	21%	32%

VIII. DISCUSSION.

The terms "mitochondria" and "Golgi apparatus" were avoided for numerous reasons.

There is no trace of either L or P granules in very young oocytes, nor do they change much in morphology or apparent chemical composition during the maturation of the egg. For these reasons they should come under the rather loose term "yolk".

The P granules differ in significant ways from mitochondria; they are more constant in size and morphology, are distributed in an unusual way in the mature egg, contain no lipide and apparently no nucleoprotein and do not stain in janus green B (although this may be due to non-penetration or slow penetration with rapid reduction).

The absence of mitochondria in young oocytes, and indeed, in all oocytes, is contrary to the theory that mitochondria are constant cell constituents. This is not, however, the first case in which mitochondria could not be identified in young oocytes,

and it would be begging the question to conclude that these cases are due to inadequate technique. A considerable literature now exists on sub-microscopic particulates in cytoplasm, and it seems likely that they are just as constant a cell constituent as the mitochondria, which they resemble closely in qualitative composition. However, there does appear to be some enzyme difference (Moog and Steinbach, 1946; Steinbach and Moog, 1945; Hogeboom *et al.*, 1946; Schneider, 1946). It may be that the microsomes can perform the functions of the mitochondria where the latter are absent, and may be transformed one into the other. Harvey (1946) has reported normal development of "mitochondria"-free *Arbacia* eggs and *de novo* formation of "mitochondria" during development of the egg.

The L granules also differ significantly from the classical Golgi apparatus; they are more resistant to fixatives, can be seen in the living cell and be stained with routine dyes. They show none of the typical complicated morphology and relations of the Golgi apparatus and none of the changes with physiological state which must be regarded as the *sine qua non* of the Golgi apparatus. Without some such criteria, there is no reason why any particulate bit of phosphatide or fatty acid should not be regarded as Golgi apparatus. The only way to establish an homology between the L granules and the Golgi apparatus would be to trace the former from the egg into the differentiated cells of the young animal, as Worley and Worley (1943), Worley (1944) and others have attempted to do. Even here the connection depends on what the author considers to be Golgi apparatus in the differentiated cell. The L granules are also different in their centrifugal properties from what is usually found for Golgi apparatus (cf. Beams, 1943; Hibbard, 1945).

IX. ACKNOWLEDGEMENTS.

The author is indebted to the C.S.I.R., Marine Biological Laboratory, Cronulla, for supply of oysters; to Mr. G. L. Kesteven for the loan of histological preparations of oyster gonads, prepared over several complete years, which gave a useful orientation to the present work; to Miss M. Dutton for technical assistance; and to Professor C. W. Stump and Dr. J. L. Still for criticism of the manuscript.

X. SUMMARY.

(1) Previous literature on pelecypod mollusc oogenesis is detailed.

(2) Methods of removing eggs from the mature ovary are described; eggs so removed are considered essentially comparable with naturally spawned eggs.

(3) An adapted Masson technique and a method of dehydration by freezing drying are described.

(4) An unusual type of definitive early auxocyte occurs.

(5) Nucleolar fragmentation is shown to be an artefact in the present material.

(6) The chromosomes may be seen at all stages of oogenesis. The diploid number is 10 and the reduction divisions occur after sperm entry.

(7) On centrifugal and cytochemical grounds, protein and lipide granules are differentiated, which are confined to the cortex and medulla, respectively, of the mature egg. Stages leading up to this are described.

(8) An external (vitelline) and an internal (plasma) cytoplasmic membrane are present.

(9) The eggs are resistant to changes in osmotic pressure and pH of the suspension medium. Of six vital dyes used only nile blue caused any staining.

(10) The Q_{o_2} (N) of fertilized and unfertilized eggs was -14 and -4.5 respectively.

(11) Centrifugal stratification of the eggs is described.

(12) Cytochemically the lipide granules consisted of phospholipide and some neutral fat. The presence of fatty acid could not be excluded.

(13) The presence of polysaccharide, probably glycogen, in the eggs is indicated.

(14) No alkaline glycerophosphatase could be demonstrated in the egg.

(15) An apparent increase in tyrosine was found in the egg protein as the cell developed, but no change in arginine could be demonstrated.

(16) The distribution of basophilia suggested that cytoplasmic ribose nucleic acid was confined to the ground cytoplasm.

(17) In general, chemical analysis confirmed cytochemical findings.

XI. REFERENCES.

BAKER, J. R., 1944.—The Structure and Chemical Composition of the Golgi Element. *Quart. J. Micr. Sci.*, 85 : 1.

BEAMS, H. W., 1943.—Ultracentrifugal Studies on Cytoplasmic Components and Inclusions. *Biol. Symp.*, 10 : 71.

BENSLEY, C. M., 1939.—Comparison of Methods for Demonstrating Glycogen Microscopically. *St. Tech.*, 14 : 47.

BENSLEY, R. R., and GERSH, I., 1933.—Studies on Cell Structure, etc. III. Nature of Mitochondria in Hepatic Cells of *Amblystoma*. *Anat. Rec.*, 57 : 217.

BERENBLUM, I., CHAIN, E., and HEATLEY, N. H., 1939.—Study of Metabolic Activity of Small Amounts of Surviving Tissue. *Biochem. J.*, 33 : 68.

BRACHET, J., 1931.—L'Evolution des Pentoses pendant le Développement de l'Oeuf d'Oursin. *C. R. Soc. Biol.*, 108 : 1167. (See also *Bull. Soc. Chem. Biol.*, 18 : 305 (1936).)

————, 1938.—La Localisation des Proteins Sulphydrilées pendant le Développement des Amphibiens. *Bull. Acad. Belg. Cl. Sci.*, 24 : 499.

COE, W. R., 1931.—Spermatogenesis in the California Oyster (*O. lurida*). *Biol. Bull.*, 61 : 309. (Also numerous papers (1930-47) mostly in *Biol. Bull.* and *J. Morph.*)

COLE, S. W., 1933.—Practical Physiological Chemistry. Heffer.

DANIELLI, J. F., and CATCHESIDE, D. G., 1945.—Phosphatase on Chromosomes. *Nature*, 156 : 294.

DAVIDSON, J. N., and WAYMOUTH, C., 1944.—Tissue Nucleic Acids. III. Nucleic Acid and Nucleotide Content of Liver Tissue. *Biochem. J.*, 38 : 379.

DOUNCE, A. L., 1943.—Enzyme Studies on Isolated Cell Nuclei of Rat Liver. *J. Biol. Chem.*, 147 : 685.

DURYEE, W. R., 1941.—The Chromosomes of the Amphibian Nucleus in "Cytology Genetics and Evolution", p. 129.

GHINST, VAN DER, 1934.—Remarques sur la Synthèse de l'Acide Thymonucleique . . . de l'Oeuf de Truite. *Arch. Biol.*, 45 : 729.

GOMORI, B., 1941.—Distribution of Phosphatase in Normal Organs and Tissues. *J. Cell. Comp. Physiol.*, 17 : 71.

HARVEY, E. B., 1941.—Vital Staining of Centrifuged *A. punctulata* Eggs. *Biol. Bull.*, 82 : 114.

————, 1946.—Structure and Development of the Clear Quarter of the *A. punctulata* Egg. *J. Exp. Zool.*, 102 : 253.

————, and LAVIN, G. I., 1944.—Chromatin in Living *A. punctulata* Egg and Cytoplasm of Centrifuged Egg, etc. *Biol. Bull.*, 86 : 163.

HIBBARD, H., 1945.—The Current Status of our Knowledge of the Golgi Apparatus in the Animal Cell. *Quart. Rev. Biol.*, 20 : 1.

HOGEBOOM, G. H., *et al.*, 1946.—Distribution of Cytochrome Oxidase in the Cytoplasm of the Mammalian Liver Cell. *J. Biol. Chem.*, 165 : 615.

HOLTFRETER, J., 1946a.—Experiments on Formed Inclusions of Amphibian Egg. I. *J. Exp. Zool.*, 101 : 355.

————, 1946b.—Id. III. Observations on Microsomes, Vacuoles and Yolk Resorption. Ibid., 103 : 81.

HUMPHREY, G. F., 1941a.—The Biology and Cultivation of Oysters in Australia. III. *Counc. Sci. Industr. Res.*, Melbourne. Pamph. No. 111.

————, 1941b.—The Determination of Glycogen in Oysters. *Aust. J. Exp. Biol. Med. Sci.*, 19 : 311.

————, 1946.—The Endogenous Respiration of Homogenates of Oyster Muscle. Ibid., 24 : 361.

JOHNSON, M. W., 1946.—A New Case of Nucleolar Extrusion. *Anat. Rec.*, 94 : 349 (suppl.).

JUST, E. E., 1939.—The Biology of the Cell Surface. Blakiston.

KAY, W. W., and WHITEHEAD, R., 1935.—The Staining of Fat with Sudan IV. *J. Path. Bact.*, 41 : 403.

KRUGELIS, E., 1942.—Cytological Demonstration of Phosphatase in Chromosomes of Mouse Testis. *J. Cell. Comp. Physiol.*, 19 : 37.

LIEBMAN, E., 1946.—On Trephocytes and Trephocytosis; a Study on the Role of Leucocytes in Nutrition and Growth. *Growth*, 10 : 291.

McRARY, W. L., and SLATTERY, M. C., 1945.—Colorimetric Determination of Pentoses and Pentosans. *Arch. Biochem.*, 6 : 151.

MITCHELL, J. S., 1943.—Disturbance of Nucleic Acid Metabolism, etc. II. *Brit. J. Exp. Path.*, 23 : 296.

MONTI, quoted in HEILBRUNN, L. V., 1943.—Outlines of General Physiology. Saunders.

MOOG, F., and STEINBACH, H. B., 1946.—Localisation of Acid and Alkaline Phosphomonoesterases in Cytoplasmic Granules. *J. Cell Comp. Physiol.*, 28 : 209.

NELSON, N., 1944.—A Photometric Adaptation of the Somogyi Method for Determination of Glucose. *J. Biol. Chem.*, 153 : 375.

OKADA, K., 1934.—Some Notes on *Musculium heterodon*. I. *Sci. Rep. Tohoku Imp. Univ.*, (4) 9 : 315.

RAFALKO, J. S., 1946.—A Modified Feulgen Reaction for Small and Diffuse Chromatin Elements. *St. Tech.*, 21 : 91.

RAI, H. S., 1931.—On the Origin of Yolk in *Ostrea cucullata*. *J. R. Micr. Soc.*, 50 : 210.

ROUGHLEY, T. C., 1933.—The Life History of the Australian Oyster (*O. commercialis*). PROC. LINN. SOC. N.S.W., 58 : 279.

SERRA, J. A., 1946.—Histochemical Tests for Proteins and Amino Acids. *St. Tech.*, 21 : 5.

SCHNEIDER, W. C., 1946.—The Intracellular Distribution of Enzymes. I. *J. Biol. Chem.*, 165 : 585.

STEINBACH, H. B., and Moog, F., 1945.—Localisation of Adenyl-pyrophosphatase in Cytoplasmic Granules. *J. Cell. Comp. Physiol.*, 26 : 175.

STONEBERG, C. A., 1939.—Lipides of Cell Nuclei. *J. Biol. Chem.*, 129 : 189.

SUBRAMANIAM, M. K., 1937.—Oogenesis of *Meretrix casta*, etc. *J. Morph.*, 61 : 127.

TENNENT, D. H., and GARDINER, M. S., 1930.—A Cytological and Biochemical Study of the Ovary of the Sea Urchin *Echinometra lucunter*. *Carnegie Pub.*, 413 : 1.

THOMAS, L. E., 1946.—A Histochemical Test for Arginine Rich Proteins. *J. Cell. Comp. Physiol.*, 28 : 145.

THOMSON, J. M., 1945.—Typescript Booklet Issued to the School in Marine Biology. Cronulla, N.S.W.

WARBURG, O., 1915.—Notizen zur Entwichlungsphysiologie des Seeigeleies. *Arch. ges Physiol.*, 160 : 324.

WHITAKER, D. M., 1931.—Rate of Oxygen Consumption by Fertilised and Unfertilised Eggs. II. *Cumingia*. *J. Gen. Physiol.*, 15 : 183.

WILLMER, E. N., 1942.—The Localisation of Phosphatase in Cells in Tissue Culture. *J. Exp. Biol.*, 19 : 11.

WILSON, E. B., 1925.—The Cell in Development and Heredity. Macmillan.

WOODS, F. H., 1932.—Keimbahn Determinants and Continuity of Germ Cells in *Sphaerium striatinum*. *J. Morph.*, 53 : 345.

WORLEY, L. G., 1943.—The Relation between the Golgi Apparatus and Droplets in Cells stainable vitally with Methylene Blue. *Proc. Nat. Acad. Sci. Wash.*, 29 : 228.

————, 1944.—Studies on Vitally Stained Golgi Apparatus. II. Yolk Formation and Pigment Concentration in the Mussel *M. Californianus*. *J. Morph.*, 75 : 77.

————, and WORLEY, E. K., 1943.—Id. I. Its Cycle in the Tectibranch Mollusc *Navanax*. Ibid., 73 : 365.

EXPLANATION OF PLATES XVI-XX.

Lettering.

a-h, Cell types A-H. ac, Anaphase chromosomes. cc, Cortex of mature oocyte. cf, Centrifugal end of cell. cp, Centripetal end of cell. ds, Vesicle detached from satellite nucleolar body. fw, Follicle wall. gc, Ground cytoplasm. kr, Karyolymph reticulum. lg, Lipide granules. lgd, Lipide granule debris. m, Medullary region of mature oocyte. mc, Metaphase chromosomes. n, Nucleolus. nf, Nucleolar fragment. ng, Nucleolar granules. nv, Vesicle produced by breakdown of germinal vesicle. pg, Protein granules. s, Nucleolar satellite. vg, Granules attached to germinal vesicle membrane. vl, Lipide in vesicular tissue. vt, Vesicular tissue.

A scale corresponding to ten microns is included in each plate. When two such scales are present, the figures to which one of them corresponds are given below or at the side of this scale. The other scale is for all other figures on the plate.

Plate xvi.

Fig. 5.—The diatom *Amphipleura lindheimeret*. This is included as a measure of technique as the experimental biologist includes standard deviations, etc.

Fig. 6.—Helly, Feulgen.

Fig. 7.—Helly, iron haematoxylin.

Fig. 8.—Bouin, Feulgen.

Figs. 9-10.—Helly, Feulgen.

Figs. 11-12.—Helly, sudan black. Nucleolar granules.

Figs. 13-15.—Post-chromated Helly, Feulgen light green.

Plate xvii.

Figs. 16-19.—1% osmic. Whole egg. Nucleolar fragmentation stages.

Figs. 20, 21, 23, 25.—Helly, Feulgen. Chromosome pairs in mature egg.

Figs. 22, 24.—Helly, Feulgen. Nucleolus chromosome relation.

Figs. 26-32.—Helly, Bensley-Cowdry.

Plate xviii.

Figs. 33-37.—Helly, Bensley-Cowdry.

Figs. 38-45.—Mann-Kopsch.

Plate xix.

Fig. 46.—Mann-Kopsch.

Figs. 47-49.—Helly, sudan black. The artefactory aggregation of L granules on the nuclear membrane in early oocytes. Compare with Figures 30, 32 and 34, remembering that there is some loss of resolution in slides mounted in low refractive index media.

Figs. 50-52.—Helly, Feulgen. Centrifuged developing whole egg. No spindle displacement. Figure 52 is unusually favourable for chromosome counts

Fig. 53.—Helly, sudan black. Centrifuged developing whole egg. The visibility of the P granules is caused by the low refractive index of the mounting medium.

Fig. 54.—Post-chromated Helly. Unhydrolysed Feulgen. The L granules stain.

Fig. 55.—Helly, sudan black.

<center>Plate xx.</center>

Figs. 56-57.—Mann-Kopsch. Mature oocyte.

Fig. 58.—Helly, sudan black.

Fig. 59.—Post-chromated Helly, sudan black.

Fig. 60.—Helly, Bensley-Cowdry. Mature oocyte.

Figs. 62-64.—1% osmic. Centrifuged mature oocytes. The deposition of osmium on the P granules is an artefact due to after treatment. It does not occur in temporary mounts but in the present figures serves to show the granule groups.

ON FOSSIL LEAVES (OLEACEAE) AND A NEW TYPE OF FOSSIL POLLEN GRAIN FROM AUSTRALIAN BROWN COAL DEPOSITS.

By ISABEL C. COOKSON, D.Sc., Department of Botany, University of Melbourne.
(*Communicated by Dr. W. R. Browne.*)

(Plates viii–x; four Text-figures.)

INTRODUCTION.

Mummified leaves, which on structural grounds are believed to have belonged to an extinct member of the family Oleaceae, occur in considerable numbers in the brown coal deposits of the Latrobe Valley in Victoria and Moorlands in South Australia (Cookson, 1946). The evidence to be submitted below suggests a possible affinity with the tribe Oleineae (Knoblauch, 1897), but is insufficient to connect them directly to an individual genus of this tribe. For this reason the generic name *Oleinites*, n. gen., which implies tribal affinities only, is proposed for them.

Two species of *Oleinites* have been discovered. One of these, namely, *O. Willisii*, n. sp., has been collected in some quantity from the upper zones of the open cut at Yallourn and in Bore 28 at 150 feet at Hazelwood, south of Morwell. *O. crenulata*, n. sp., the second species, has been found only in the deposits at Moorlands.

Ettingshausen in 1888 described a fossil leaf from Vegetable Creek in New South Wales to which the name *Olea Macintyrei* was given. His identification, however, was not substantiated by anatomical details. Apart from this doubtful species, I know of no other record of fossil Oleaceae from southern Tertiary rocks.

The fossils typifying *Oleinites* are glossy, transparent, and paper-like in appearance and greenish-brown to amber in colour. Although nothing remains of the original structure but the outer wall of the epidermal cells, the general form of the leaves is faithfully preserved. Frequently the thicker upper cuticle alone is represented, but in more favourable examples useful portions of the lower cuticle have been found. The thickness and high degree of cutinization of the outer walls of the epidermal cells were apparently responsible for the excellent preservation of both morphological and anatomical features.

Usually *O. Willisii* is aggregated into thick, layered masses in the coal (Plate viii, fig. 1), from which individual leaves or pieces of leaves can be readily detached. *O. crenulata*, on the other hand, is more sparsely distributed in the coal and is preserved in a more fragmentary condition. For this reason, *O. Willisii* has been chosen as the type species of the new genus.

Portions of such fossils can be mounted directly either in Canada Balsam or glycerine jelly, but clearer and cleaner preparations have been obtained by bleaching for about fifteen to thirty minutes in a 12% solution of sodium hypochlorite. Treated cuticles, after a thorough washing with water, can then be stained with safranin and mounted in glycerine jelly.

DESCRIPTION OF FOSSILS.

OLEINITES WILLISII, n. gen., n. sp.

External Features. Plate viii, figs. 1–5.

The leaves are simple, shortly petiolate, and oblanceolate to almost spathulate. They show a considerable variation in size, the examples measured ranging from 1–9 cm. in length and 2 mm.–2·3 cm. in width. They have an obtuse and usually more

O

or less deeply retuse apex and an entire and strongly thickened margin. Apart from
the midrib, which is indicated on both surfaces, the venation is not evident.

Peltate Hairs. Plate ix, fig. 8; Plate x, fig. 24.

Trichomes which seem to come into the category of peltate hairs are conspicuous
features of both leaf surfaces. Their state of preservation permits the interpretation
of their general form, but precludes a clear and positive statement regarding the finer
details of structure. Furthermore, it is impossible to say whether these hairs had a
glandular function or were more comparable to "clothing hairs" such as occur, for
example, in *Olea europaea* (Solereder, 1908, p. 523). Nevertheless, it should be
mentioned here that the frequent occurrence of epiphyllous fungi on such leaf remains
might be more compatible with a glandular character. Because of this uncertainty
regarding their function they will be referred to subsequently as peltate hairs.

Each peltate hair consisted of a stalk and a radially constructed shield of variable
size. The stalk itself is never preserved, but its upper limit is clearly marked by a
circular thickening 18–30μ in diameter, beneath and in the centre of the shield.
Moreover, the fact that it was sunk beneath the general level of the cuticular surface
is shown by a small elevation in the vicinity of each hair, which is plainly visible
when a cuticular surface is viewed from within (Plate viii, fig. 7). The position of the
hairs is indicated by corresponding depressions on the coal when the fossil is removed.

The shield was apparently composed of radiating cylindrical cells with cutinized
walls and wide lumina, but the latter are usually preserved in a more or less contracted
condition. The number of rays varies from sixteen to thirty-six or possibly even more,
according to the size of the shield. In the majority of hairs, the diameter of the
shield ranges from 58–106μ, the average being approximately 80μ. However, con-
siderably larger hairs, the diameter of which is between 119–186μ, occur at intervals,
particularly on the midrib. In these examples it is difficult to determine with accuracy
either the number or arrangement of the cells into which the shield is divided. The
ray-cells appear to have been free from one another for the greater portion of their
length. This may have been a natural feature, but the possibility that the apparent
disunion resulted from *post mortem* changes must also be borne in mind. The length
of the individual cell is exceedingly variable and only a few reach the centre of the
shield, the majority ending at the margin of the stalk (Text-fig. 3). The appearance
of some of the hairs suggests that a second smaller shield composed of small, free
ray-cells may have been present on the upper surface of the principal shield.

Lower Epidermis. Plate ix, figs. 9–11.

The stomata are restricted to the lower epidermis, where they assume a more or
less linear grouping around, and at some distance from, the peltate hairs. The
approximate number per sq. mm. is 100 ± 40. They are oval to circular in surface
view, and usually distinctly flattened at the poles. The considerable variation in size
of the stomata, which is especially evident in *O. Willisii*, is possibly the most distinctive
and reliable diagnostic feature of *Oleinites*. In this species, stomata of three quite
arbitrary size groups can be recognized. The majority come within the limits of
29–58μ for the axis parallel to the pore (to be subsequently referred to as the length),
and 26·6–58μ for the axis which crosses the pore (the width), the approximate average
for this group being 46 × 44μ. Larger stomata, which occur sporadically on the lamina,
comprise the second group; they have a range of from 61–85μ × 53–80μ, and an average
of 72 × 69μ. Giant stomata, usually restricted to above or near the midrib, are more
sparingly developed. Those observed have measured from 93–119μ in length and 53–112μ
in width.

The outer walls of the guard cells are strongly thickened, and in the larger stomata
show clearly defined concentric cuticular striations. The dorsal limits of the guard
cells are sharply defined, and the poral rims are pronounced. The epidermal parenchyma
can seldom be distinguished, even in otherwise favourable cuticles. With low-powered
objectives the outlines of the cells surrounding the hair bases are sometimes visible.
These are of moderate size and have thin, deeply sinuous lateral walls. The outer
wall is thickened and cutinized, but to a lesser degree than that of the upper epidermis.

The peltate glands conform to the general description already given; they are rather widely spaced, the approximate number per sq. mm. being 9.

Upper Epidermis. Plate ix, fig. 8.

This consists of uniform, sinuate parenchyma; the outer cell walls are about 13μ thick and heavily cutinized. Peltate hairs, similar to those on the lower epidermis, are present, where they average 10 per sq. mm.

OLEINITES CRENULATA, n. sp.

External Features. Plate x, figs. 16–21.

A complete leaf cuticle of this species has not been seen, but a workable description permitting its identification has been built up by a study of a number of the larger fragments of cuticle.

The leaves of *O. crenulata* seem to have varied considerably in size, for the smallest specimen observed measures 1 cm. in length and 0·5 cm. in width, and the larger, incomplete specimen, illustrated in Plate x, figure 16, is 2·5 cm. long and 1·8 cm. wide. The lamina which appears to have been broadly lanceolate tapers towards the base. In several fragments the apex varies from obtuse to subacute, and is sometimes slightly retuse (Plate x, fig. 17). The margin of the leaf is unthickened, and in the distal region, at least, is slightly crenulate. The venation is prominent on both surfaces; from the midrib strong lateral veins are given off at an angle of about 75°, and these give rise to numerous finer veins which anastomose to form a conspicuous network. This is indicated on the upper surface by irregular, raised areas, each of which is separated by the slightly sunken cuticle covering the venules.

Lower Epidermis. Plate x, figs. 25, 26.

The stomata occur only on the lower epidermis, where they are restricted to the areas marked out by the veins. Here they are closely arranged and number about 450 per sq. mm. They are oval to circular in surface view and average 35μ × 32μ, their range in length being 24–50μ. Much larger stomata occur infrequently; these vary from 53–106μ in length and from 37–101μ in width. The dorsal limits of the guard cells are clearly defined and their outer walls are concentrically striated. The poral rims, which are frequently missing, however, do not appear to have been especially thickened.

The cuticle of the stomatal parenchyma is seldom preserved, and in one specimen only have the deeply sinuous outlines of epidermal cells been distinguished (Plate x, fig. 26). The parenchyma appears to have been uniform and the outer walls of the epidermal cells non-striated. The cuticle of the elongated cells covering the veins, however, is longitudinally striated. Peltate hairs of the same general type as those of *O. Willisii* are rather widely spaced in the lower cuticle.

Upper Epidermis. Plate x, figs. 23, 24.

The cells of the upper epidermis are large and deeply sinuate; the cuticle shows undulating striations which follow, more or less, the outlines of the cells. Peltate hairs average 20 ± 13 per sq. mm.; their shields have diameters ranging from 53–128μ and the number of rays into which they are divided varies from 12 in the smallest to about 36 in the largest examples. The rays lie in one plane, but all do not reach the centre (Plate x, fig. 24).

SYSTEMATIC POSITION OF OLEINITES.

The identification of fossil leaves, even when structural features enable comparisons with living types to be made, is often associated with an element of doubt, and such is the case in the present instance. No recent type has been found having a cuticular structure with which that of *Oleinites* can be exactly matched. When, however, individual features of the fossil cuticles are compared with similar characters in recent species, the number of points on which agreement is reached is sufficient strongly to favour, if not definitely to establish, an alliance with the Oleaceae in general and the Oleineae in particular. The facts that support such taxonomy are summarized as follows:

(a). *Size and Shape of Stomata.*—Perhaps the most striking feature of the lower cuticles of *Oleinites*, as exemplified by *O. Willisii* and *O. crenulata*, is the wide range in size shown by the stomata. Furthermore, the development of exceedingly large stomata, which sometimes reach a length of 119μ, is both obvious and characteristic. It was this unusual feature that originally suggested the Oleaceae as the family to which *Oleinites* might be related. Solereder (loc. cit., p. 522) writes: "It is also worthy of remark that sometimes, e.g. *Forestiera porulusa*, large and small stomata occur side by side." This statement fitted so well with the appearance of *Oleinites* that cuticles of some of the other members of the tribe Oleineae were examined. The figures obtained show that of the recent species examined 65% of the species of *Olea* and 100% of those of *Notelaea* possess a variable number of stomata which are conspicuous on account of their greater size and isolated position. The length of such "large" stomata exceeds the average length of the smaller stomata by from $5-20\mu$. Moreover, even when large stomata, as such, are indistinguishable, a variation in length of from $7-20\mu$ is a natural occurrence in all of the species investigated. In spite of lower maxima and minima, therefore, the range in length is comparable to that of *Oleinites*.

As far as actual size is concerned, the stomata of *Oleinites*, especially *O. Willisii*, appear to be quite unusual. The large stomata of *O. concolor*, for example, which average $60 \times 40\mu$, fall far short of the dimensions of the large stomata of *O. Willisii*. The stomata of *O. crenulata*, being smaller, are more comparable with those of recent species, but here again giant stomata far above the average distinguish this species from recent types.

The shape of the stomata in species of *Olea* and *Notelaea*, since it varies from elliptical to circular according to the species, is a less important diagnostic character. In *Oleinites* the stomata are oval to circular in surface view and in this respect approximate to those of *O. acuminata*, *O. maritima*, *O. dioica*, *N. longifolia* and *N. ovata*, in all of which the stomata are roughly circular.

Great variation in the grouping of the stomata has been observed. In the majority of recent species the stomata are more or less evenly distributed but are usually wanting over the veins (in *O. foveolata*, as in *Oleinites Willisii*, large stomata are sparsely developed over the midrib), and in the immediate vicinity of the trichomes and large stomata. Sometimes, e.g., in *O. paniculata* a wider zone around each hair is devoid of stomata, a feature reminiscent of *O. Willisii*. The somewhat linear arrangement of the stomata in this species and in *O. foveolata* is another point of convergence.

(b). *Peltate Trichomes.*—These are present, according to Solereder (loc. cit., p. 521), in all genera of the Oleaceae, but this author does not mention whether they are constantly distributed on both sides of the leaves. During
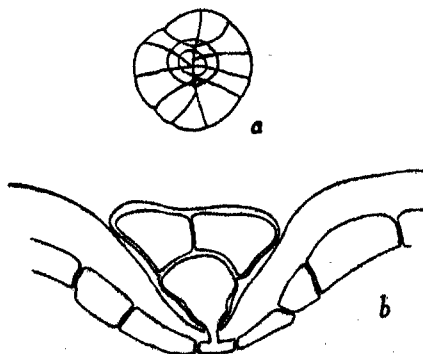
Text-fig. 1.—(a). Peltate gland of *Olea foveolata* in surface view, × 500.   (b). Peltate gland of *Olea lanceolata* in vertical section, × 500.

the present investigation peltate trichomes have been found invariably on the under epidermis, and with only one exception, namely, *O. foveolata*, on the upper epidermis. Peltate hairs have been recorded in a number of families and genera (Solereder, p. 1121), but in many of these, appear to be restricted to the lower epidermis. Their occurrence on both cuticular surfaces of *Oleinites*, though in itself insufficient evidence of affinity with the Oleaceae, corroborates the assignment to this family.
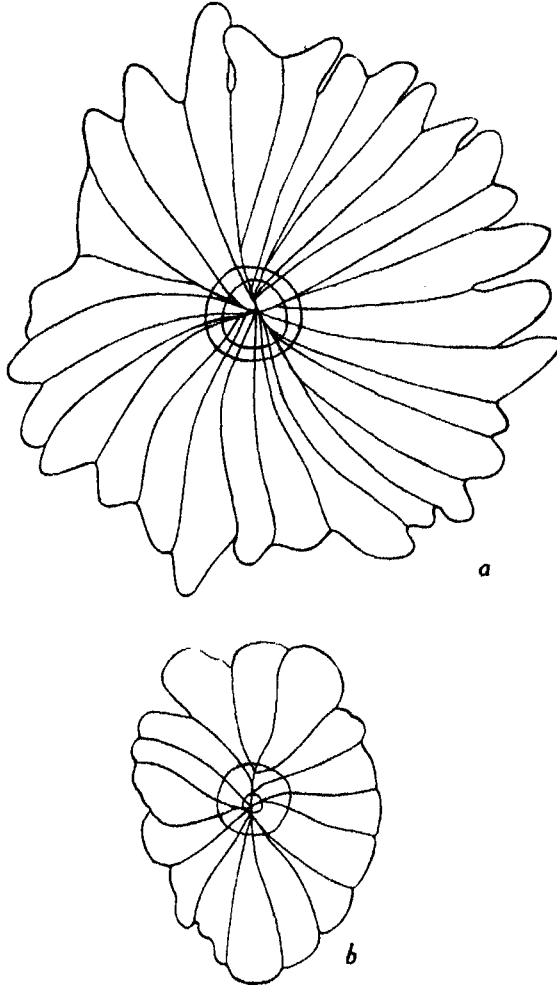
Text-fig. 2.—Peltate hairs of (*a*) *Olea europaea* and (*b*) *Olea paniculata*. × 500.

In most recent members of the Oleaceae the trichomes take the form of peltate glands (Prillieux, 1856). In these the head ranges from 29–60μ; it is oval to spherical with usually an entire margin, and is divided into from 8–16 cells. In contrast are the "clothing hairs" of Solereder which distinguish such species of *Olea* as *O. europaea*, *O. chrysophylla* and *O. cuspidata*. In these species the shields, which are divided into 24–30 partially separated cells, are large, the average diameter being about 160μ; moreover, they overlap one another so that an effective covering for the leaf-surface is provided. In a few species, e.g., *O. paniculata*, *O. glandulifera* and *O. exasperata*, an intermediate type both as regards size and distribution appears to be distinguishable. The

average diameters of the shields of these species vary from 80–90μ and are so spaced that they do not overlap one another; in addition the ray-cells, which number 16–20, are usually completely united. It is not possible to decide from herbarium specimens whether this type is of the nature of small clothing hairs or large peltate glands, so that, for convenience, they will be arbitrarily termed peltate hairs.

As regards the size of the peltate hairs of *Oleinites*, the most remarkable feature, when comparisons with recent species are made, is the extreme difference in size of the shields of the largest and smallest hairs. The large hairs with shields ranging between 100 and 186μ come within the range of those of the *O. europaea* class, but the majority have diameters considerably below these figures. The average diameter of the smaller hairs in *O. Willisii* is 80μ and in *O. crenulata* 70μ, both examples coming within the range of the *O. paniculata* type. In no species of either *Olea* or *Notelaea* has such a wide difference been observed; in fact it can be said of recent species that the range in size is not considerable. Reference has already been made to the difficulty experienced in interpreting the structure of the hairs of *Oleinites*. Whilst they appear to have been built on the same general plan as those of the *O. europaea* and *O. paniculata* types, their greater variability both in size and number of rays, together with the apparently greater freedom of the ray-cells and the higher degree of cutinization of their walls, distinguishes them from the peltate hairs of recent species.

(c). *Epidermal Parenchyma.*—In the majority of recent Oleineae the cells of the epidermal parenchyma have straight lateral walls. A few, however, such as *O. foveolata, O. vitiensis* and *O. montana*, agree with *Oleinites* in having epidermal cells with undulating lateral walls.

Solereder (loc. cit., p. 522) notes for leaves of the Oleaceae that "the outer walls of the epidermal cells are distinguished by considerable thickness". This feature, shown well by *O. lanceolata* and *O. verrucosa*, where the wall may be as much as 26μ thick, also characterizes *Oleinites*, more particularly *O. Willisii*, in which the upper cuticle is about 13μ thick. Solereder continues with the remark that "the cuticle not uncommonly shows undulated striation". Personally, I have observed clearly defined striations in the upper cuticles of such species as *Olea exasperata, O. lanceolata, Notelaea ligustrina* and *N. longifolia*. An interesting comparison is thus afforded with *Oleinites crenulata*, in which the upper cuticle is conspicuously striated, the striations following, more or less, the sinuous outlines of the cells themselves. The cuticle of the cells of the lower surface which cover the venules show longitudinal striations.

(d). *External Morphology.*—The leaves of the Oleineae are simple, entire, petiolate and vary considerably in size within a species. This description applies equally well to the two fossil species, a wide size-range being apparent in both.

The prominence of the venation is another variable character. In *Olea cuspidata* and *O. exasperata*, for example, as in *Oleinites Willisii*, the midrib is the only vein clearly distinguishable on both sides of the leaf. Bentham (1869, p. 298) makes use of this character in his key to the Australian species of *Notelaea*, to distinguish *N. ligustrina* and *N. linearis* from the remaining species in which a reticulum is conspicuous. On the other hand, the prominent network of *Oleinites crenulata* is paralleled amongst the Oleas by the somewhat finer and less obvious reticulum of *O. paniculata*.

The retuse apex of *O. Willisii* is remarkably similar to that of *Osmanthus Badula*, although the slight narrowing towards the apex in that species contrasts with the usually broader tip of *O. Willisii*. This resemblance is only of minor importance, however, since retuse apices occur in widely divergent families.

The last morphological character that must be briefly mentioned is the thickened leaf-margin of *O. Willisii*. It is interesting to find the counterpart

of this in the thickened "nerve-like" margin of *Notelaea linearis* mentioned by Bentham (loc. cit., p. 300) and to see it prominently developed also in *Osmanthus Badula* (Plate viii, fig. 6) and *Olea exasperata*.

(e). *Geographical Distribution.*—The Oleineae is well represented in the recent floras of Australia, Polynesia and New Zealand. Five species of *Olea* have been recorded from this area, one, namely, *Olea paniculata*, being endemic to Australia. Several species of *Notelaea* also occur in the Australasian Region, five of which are Australian species. Without entering into greater details, therefore, it is clear that the present distribution of the Oleineae is consistent with the tentative suggestions put forward in this paper regarding the taxonomy of *Oleinites*.

CUTICULAR STRUCTURE OF SOME RECENT OLEINEAE.

This section has been prepared with the assistance of Miss S. Duigan, B.Sc., whose willing co-operation I acknowledge with much pleasure; I am further indebted to Miss Duigan for the drawings shown in Text-figures 1–4. Thanks are also due to Mr. A. W. Jessep, Director of National Herbarium of Victoria, for providing the specimens used in this study.

The cuticles were removed by the action of a warm 12% solution of sodium hypochlorite, after a previous boiling in water to soften the dried tissues.

1. AVERAGE DIAMETER OF PELTATE HAIRS 100-180μ.
Olea europaea Linn. Mediterranean Region.

Lower Epidermis.—Cells small, lateral walls thin, unpitted, slightly sinuous; cuticle thin, faintly striated. Stomata about 300 per sq. mm., absent from the parenchyma over the veins and immediately surrounding the hair bases; elliptical, averaging 28 × 21μ, the long diameter ranging from 26–33μ. Large stomata average 37 × 19μ, and range from 37–41μ long. Peltate hairs are extremely numerous, averaging 180 per sq. mm.; each shield is divided into about 24–30 cells which become free from one another towards the periphery; the average diameter is 160μ, and the scales overlap.

Upper Epidermis.—Cells small, lateral walls thin, straight and unpitted. Glands average 50 per sq. mm.

Olea chrysophylla Lam. Abyssinia.

Lower Epidermis.—Cells small, lateral walls thin, straight, unpitted. Stomata about 340 per sq. mm., evenly distributed, elliptical, averaging 21 × 15μ, long axis 18–26μ. Large stomata not developed. Peltate hairs numerous, 160 per sq. mm.; shield about 118μ in diameter, composed of 24 rays which become free at the periphery.

Upper Epidermis.—Cells small, lateral walls moderately thick, straight, and unpitted; cuticle granular; peltate hairs average 46 per sq. mm.

Olea cuspidata Well. India.

Lower Epidermis.—Cells small, lateral walls thin, unpitted, slightly sinuous. Stomata evenly distributed, approximately 330 per sq. mm.; elliptical, averaging 23 × 16μ, with a range in length of 18–26μ. Large stomata not differentiated. Peltate hairs numerous, overlapping, approximately 160 per sq. mm.; shield divided into 24 rays, which become free near the periphery; average diameter 124μ.

Upper Epidermis.—Cells of medium size, lateral walls thin, sinuous, unpitted; those immediately adjacent to the stalks of the hairs larger, with straighter walls. Peltate hairs average 57 per sq. mm.

2. AVERAGE DIAMETER OF PELTATE HAIRS 80-100μ.
Olea exasperata Jacq. South Africa.

Lower Epidermis.—Cells of medium size, lateral walls straight, thick, unpitted; outer walls thick; cuticle granular. Stomata evenly distributed, approximately 200 per sq. mm.; broadly elliptical in shape, average size 34 × 26μ, the long axis ranging from 26–37μ. Large stomata average 53 × 37μ, and range in length from 44–59μ. Venules

Text-fig. 3.—(a). Peltate hair of *Oleinites crenulata* in surface view, × 600.   (b). Vertical section of lower cuticle of *Oleinites Willisii* showing peltate hair, × 600.

are absent. Peltate hairs average 33 per sq. mm.; the shield is divided into 16 unequal rays; margin entire, sinuous; average diameter 80μ.

Upper Epidermis.—Cells of medium size, lateral walls thick, straight, and unpitted; cuticular striations conspicuous; glands sparse, averaging 8 per sq. mm.

Olea glandulifera Desf.   India.

Lower Epidermis.—Cells small, lateral walls thin, straight, unpitted, those adjoining the bases of the hairs being larger. Veins conspicuous. Stomata approximately 370 per sq. mm., absent from the parenchyma covering veins and surrounding the hairs and large stomata. Elliptical in shape, averaging 26 × 20μ, the long axis ranging from 22–30μ. Large stomata average 38 × 27μ and range from 36–44μ. Peltate hairs numerous, approximately 85 per sq. mm.; shield more or less circular in shape, composed of 16–20 unequal rays; average diameter 84μ.

Upper Epidermis.—Cells large, lateral walls thin, slightly sinuous, pitted; cuticle granular, peltate hairs moderately numerous, approximately 45 per sq. mm.

Olea paniculata R.Br.   Queensland.

Lower Epidermis.—Cells small, lateral walls thin, slightly sinuous, unpitted; cuticle thin and faintly striated. Stomata about 250 per sq. mm., unevenly distributed, absent from parenchyma covering the venules and around the glands; narrowly elliptical, with average diameters of 25 × 17μ, and a range in length of 22–30μ. Large stomata average 35 × 23μ, and range in length from 33–41μ. Peltate hairs about 33 per sq. mm. Scale more or less circular in outline, with an entire margin; divided into 16 cells; average diameter 90μ.

Upper Epidermis.—Cells of medium size, lateral walls thin, sinuous, and unpitted. Peltate hairs about 13 per sq. mm.

3. AVERAGE DIAMETER OF PELTATE GLANDS UNDER 60μ.
Olea acuminata Wall.   India.

Lower Epidermis.—Cells small, lateral walls moderately thick, slightly sinuous, unpitted; two rows with straight walls arranged radially around each gland; cuticle faintly granular. Stomata very numerous, averaging 850 per sq. mm.; small, approxi-

mately circular, the average being 19 × 20μ, and the range in length 15–26μ. Large stomata very sparse, when present, restricted to parenchyma above the veins; elliptical, averaging 32 × 24μ, with a range in length of 28–36μ. Peltate glands infrequent, approximately 12 per sq. mm.; head oval, with an entire margin; divided into 8 cells, those on either side meeting at a median line; average diameter 35μ.

Upper Epidermis.—Cells small, lateral walls moderately thick, slightly sinuous, and unpitted. Glands very sparsely developed, approximately 3 per sq. mm.

Olea apetala Vahl. New Zealand.

Lower Epidermis.—Cells small, lateral walls thick, slightly sinuous, unpitted. Cells radially arranged around the bases of the glands and the large stomata. Stomata absent from venules and vicinity of glands; approximately circular, averaging 25 × 23μ, with a range of 22–27μ. T-shaped thickening present at junction between guard cells. Large stomata, elliptical; average size 35 × 26μ, range in length from 34–41μ. Peltate glands about 11 per sq. mm., head approximately circular, divided into 8 irregular rays; average diameter 43μ.

Upper Epidermis.—Cells moderately large, lateral walls thick, slightly sinuous, and pitted. Glands approximately 4 per sq. mm.

Olea capensis Linn. South Africa.

Lower Epidermis.—Cells of medium size, lateral walls thick, straight, unpitted. Stomata approximately 110 per sq. mm., absent from parenchyma covering veins and surrounding glands and large stomata; elliptical, averaging 33 × 22μ; range of the long axis 22–37μ. Large stomata distinct, averaging 52 × 28μ, long axis ranging from 38–59μ. Peltate glands very sparsely developed, approximately 3 per sq. mm. The head is divided into 12 rays, and has a slightly wavy margin; the average diameter is 46μ.

Upper Epidermis.—Cells medium, with thick, straight, unpitted walls. Glands very sparse, approximately 1 per sq. mm.

Olea concolor E. Mey. South Africa.

Lower Epidermis.—Cells small, lateral walls thick, straight, unpitted, outer wall thick, undulant. Stomata evenly distributed, approximately 130 per sq. mm., elliptical in shape, averaging 39 × 30μ, with a range in length of 26–44μ. Large stomata averaging 60 × 40μ, with a range in length of 56–67μ, particularly conspicuous near the midrib. Peltate glands approximately 33 per sq. mm.; head, 47μ in diameter, divided into about 16 rays of slightly irregular length.

Upper Epidermis.—Cells large, lateral walls rather thin, straight, sparsely pitted. Glands approximately 13 per sq. mm.

Olea Cunninghami Hook. New Zealand.

Lower Epidermis.—Cells small, arranged radially in one row around the bases of the glands; lateral walls moderately thick, straight, unpitted. Stomata approximately 450 per sq. mm., absent from the veins and the vicinity of the glands; elliptical with flattened poles, average size 26 × 22μ, with a range in length of 22–33μ. Polar T-shaped thickening present. Peltate glands approximately 47 per sq. mm., heads oval, entire, each divided by exceedingly thin walls into 8 rays; average diameter 41μ.

Upper Epidermis.—Cells small, lateral walls moderately thick, straight, pitted; cuticle irregularly reticulate. Glands approximately 35 per sq. mm.

Olea dioica Roxb. India.

Lower Epidermis.—Cells small, lateral walls thin, slightly sinuous, unpitted; cells bordering glands more or less radially arranged; cuticle granular. Stomata, absent from the immediate vicinity of glands and large stomata, approximately 330 per sq. mm. Elliptical to almost circular, average 24 × 20μ, with the long axis ranging from 22–26μ; T-shaped thickening conspicuous. Large stomata average 32 × 26μ, and have a long axis ranging from 30–33μ. Peltate glands aproximately 39 per sq. mm.; heads elliptical to circular, with even margins, each with 8 faintly defined rays; average diameter 25μ.

Upper Epidermis.—Cells small, lateral walls thin, slightly sinuous, unpitted; cuticle granular; peltate glands average 12 per sq. mm.

Olea foveolata E. Mey.   South Africa.

Lower Epidermis.—Cells medium, lateral walls thin, sinuous, unpitted.   Cells bordering glands and large stomata radially arranged, with thicker, straighter walls; cuticle faintly granular.   Stomata arranged in irregular lines; approximately 210 per sq. mm.; elliptical, averaging 29 × 23μ, with a range in length of 26–33μ.   Large stomata rare, sparsely present on midrib, 37 × 17μ, with a range of the long axis of 37–41μ. Peltate glands very infrequent, approximately 2 per sq. mm.; heads oval, 16 celled, with an average diameter of 42μ.   Short broad, thick-walled, sharply pointed hairs, 95μ in length, are sparsely developed.

Upper Epidermis.—Cells small, lateral walls thick, somewhat sinuous, pitted.   Glands and hairs absent.

Olea lanceolata Hook. f.   New Zealand.

Lower Epidermis.—Cells of medium size, arranged radially around the bases of the glands; lateral walls thick, straight, unpitted; outer wall thick.   Cuticle finely striated.   Stomata about 160 per sq. mm.; elliptical, averaging 40 × 27μ, with the long axis ranging from 26–48μ.   Large stomata not distinguishable.   Peltate glands about 12 per sq. mm., occasionally forming small compact groups; head circular, divided into 16 cells; average diameter 48μ.

Upper Epidermis.—Cells small, lateral walls thick, straight, and unpitted; cuticle thick, undulated striation conspicuous.   Glands very sparse, about 3 per sq. mm.

Olea maritima Wall.   Malaya.

Lower Epidermis.—Cells of medium size, those around the glands and large stomata radially arranged and with straight walls, the remainder with thin, sinuous, unpitted lateral walls; cuticle granular to striated.   Stomata approximately 290 per sq. mm.; absent from the parenchyma covering the veins and in the vicinity of the glands and large stomata; elliptical to circular, averaging 24 × 20μ, long axis ranging from 19–30μ. Large stomata average 33 × 21μ, and vary in length from 30–37μ.   Peltate glands about 43 per sq. mm.; head roughly circular in outline, divided into 8 slightly unequal cells; average diameter 27μ.

Upper Epidermis.—Cells of medium size, lateral walls moderately thick, slightly sinuous, unpitted; cuticle faintly granular.   Glands average 26 per sq. mm.

Olea montana Hook f.   New Zealand.

Lower Epidermis.—Cells of medium size, slightly larger and thicker walled near the glands; lateral walls thin, slightly sinuous, unpitted; cuticle irregularly reticulate. Stomata about 240 per sq. mm., absent from parenchyma over the veins and in the immediate vicinity of glands and large stomata; elliptical, with flattened poles; average size 30 × 26μ, range in length 26–33μ; T-shaped thickening present.   Large stomata average 41 × 27μ; length range 37–52μ.   Peltate glands sparse, about 6 per sq. mm.; head oval to circular, divided into 12 cells; average diameter 46μ.

Upper Epidermis.—Cells large, lateral walls thin, sinuous, unpitted; cuticle granular to striated.   Glands about 5 per sq. mm.   Unicellular pointed hairs developed on the parenchyma over the veins.

Olea myrtifolia Wall.   India.

Lower Epidermis.—Cells small, lateral walls thin, straight, unpitted; outer wall thin.   Stomata approximately 570 per sq. mm., absent from parenchyma covering the veins; elliptical in shape, averaging 23 × 16μ, long axis ranging from 19–33μ.   Peltate glands approximately 8 per sq. mm., oval to circular, divided into 8 rays, margin entire; average diameter 29μ.

Upper Epidermis.—Cells small, lateral walls thick, straight and pitted; cuticle faintly striated.   Glands very sparse—about 1 per sq. mm.

Olea polygama Wight. Ceylon.

Lower Epidermis.—Cells moderately large, with thin, somewhat sinuous, unpitted walls; cuticle striated. Stomata approximately 250 per sq. mm.; elliptical, averaging 26 × 21μ, the long axis ranging from 22–30μ; T-shaped polar thickening present. Large stomata prominent, occurring principally over the veins; average size 41 × 29μ, the long axis ranging from 37–48μ. Peltate glands sparsely developed, approximately 7 per sq. mm.; heads circular, often somewhat flattened; usually divided into 8 component cells; margin entire; average diameter 46μ.

Upper Epidermis.—Cells small, lateral walls moderately thick, straight, unpitted; cuticle faintly granular. Glands sparse, 2 per sq. mm.

Olea robusta Sweet. India.

Lower Epidermis.—Cells small, arranged radially around the bases of the glands; lateral walls moderately thick, straight, unpitted; cuticle faintly striated. Stomata approximately 420 per sq. mm., wanting over the venules and near the glands; broadly elliptical, averaging 25 × 20μ, with a range in length of 19–30μ. Large stomata average 34 × 27μ and range in length from 33–37μ. Peltate glands sparse, about 9 per sq. mm.; head approximately circular, divided into 8 slightly unequal cells; average diameter 35μ.

Upper Epidermis.—Cells moderately large, lateral walls thin, straight, and pitted. Glands very sparse, about 2 per sq. mm.

Olea sandwicensis A. Gray. Hawaii.

Lower Epidermis.—Cells small, radially arranged around the glands; lateral walls thick, straight, unpitted; outer wall thick. Stomata approximately 280 per sq. mm., absent from parenchyma over veins and immediately surrounding glands; elliptical, averaging 26 × 20μ, the long axis ranging from 19–30μ. T-shaped thickening faintly indicated. Large stomata 36 × 27μ, range in length 33–41μ. Peltate glands about 34 per sq. mm.; head roughly circular, divided into 8 rays; average diameter 56μ.

Upper Epidermis.—Cells small, lateral walls thick, slightly sinuous, unpitted. Glands sparse, about 8 per sq. mm.

Olea verrucosa Link. South Africa.

Lower Epidermis.—Cells small, lateral walls thick, straight, unpitted; outer wall very thick. Stomata about 220 per sq. mm.; elliptical, average size 35 × 28μ, with a range in length of 26–50μ. Glands approximately 17 per sq. mm.; heads missing in the material available for examination.

Upper Epidermis.—Cells of medium size, lateral walls thick, straight, unpitted; outer wall thick—26μ. Glands 5 per sq. mm.

Olea vitiensis Seem. Tonga I.

Lower Epidermis.—Cells of medium size, lateral walls thin, sinuous, unpitted. Stomata about 130 per sq. mm., unevenly distributed, absent from midrib; elliptical to somewhat circular, average size 27 × 20μ, with a range in length of 26–33μ. Large stomata not differentiated. Peltate glands about 32 per sq. mm.; head roughly circular, divided into 12 cells; average diameter 48μ.

Upper Epidermis.—Cells of medium size; lateral walls moderately thick, slightly sinuous, unpitted. Glands very sparse, about 1 per sq. mm.

Notelaea ligustrina Vent. Tasmania.

Lower Epidermis.—Cells of medium size, arranged radially around glands and large stomata; lateral walls thin, straight, unpitted; cuticle striated. Stomata approximately 220 per sq. mm., absent over the veins and the immediate vicinity of glands and large stomata; elliptical, average size 32 × 21μ, the long axis ranging from 26–37μ. Large stomata average 43 × 24μ, with a range in length of 41–44μ. Peltate glands infrequent, approximately 15 per sq. mm.; the head oval with an entire margin, irregularly divided into from 8–14 cells; average diameter 53μ.

Upper Epidermis.—Cells moderately large, lateral walls thick, straight, unpitted; cuticular striations faint and irregular. Glands average 3 per sq. mm.

Notelaea linearis Benth. New South Wales.

Lower Epidermis.—Cells medium, radially arranged around the bases of the glands; lateral walls rather thin, straight, unpitted. Stomata average 250 per sq. mm., absent from the parenchyma above the veins and in the immediate vicinity of the glands and large stomata; broadly elliptical, averaging 31 × 26μ, with a range of 30–33μ. Large stomata average 39 × 29μ, with a range in length of 37–41μ. Peltate glands about 15 per sq. mm., head approximately circular with an entire margin, divided into 12 irregular rays; average diameter 38μ.

Upper Epidermis.—Cells moderately large, with thick, straight, unpitted walls; cuticle faintly granular. Glands very few, averaging 3 per sq. mm.

Notelaea longifolia Vent. Victoria.

Lower Epidermis.—Cells small, radially arranged around the bases of the glands; lateral walls thin, straight, unpitted; cuticle striated. Stomata approximately 810 per sq. mm., almost circular, averaging 22 × 21μ, and ranging in length from 17–24μ; T-shaped thickening present. Large stomata average 27 × 25μ, and range in length from 27–29μ. Peltate glands approximately 22 per sq. mm.; head elliptical to circular, divided into 8 unequal cells; average diameter 35μ.

Upper Epidermis.—Cells of medium size, lateral walls thick, straight, unpitted; cuticle striated. Glands approximately 14 per sq. mm.

Notelaea ovata R.Br. New South Wales.

Lower Epidermis.—Cells small, those around the hair bases and large stomata radially arranged; lateral walls thick, straight, unpitted; outer wall thick. Stomata average 450 per sq. mm., absent from parenchyma over venules and immediate vicinity of glands; approximately circular, average size 23 × 22μ, with a range in length of 19–27μ; T-shaped thickening conspicuous. Large stomata average 34 × 22μ, and range in length from 31–36μ. Peltate glands about 16 per sq. mm.; the head elliptical to circular, divided into 8 unequal cells; average diameter 35μ. Slightly curved, unicellular hairs numerous.

Upper Epidermis.—Cells of medium size, lateral walls thick, straight and unpitted, outer walls thick. Glands very sparse, averaging 4 per sq. mm. Unicellular, slightly curved, hairs present.

Notelaea punctata R.Br. Queensland.

Lower Epidermis.—Cells small, somewhat radially arranged around the bases of the glands; lateral walls thin, straight, unpitted; outer wall thick. Stomata about 510 per sq. mm., absent from parenchyma over the veins and around the glands. Elliptical to circular, from 22–30μ long, averaging 26 × 22μ. Large stomata average 31 × 20μ, and range from 29–34μ. Peltate glands about 22 per sq. mm.; head, roughly circular with an even margin, divided into 8 cells; average diameter 29μ.

Upper Epidermis.—Cells of medium size, lateral walls thin, slightly sinuous, unpitted; cuticle granular. Glands about 6 per sq. mm.

Linociera Wightii C. B. Clarke. India.

Lower Epidermis.—Cells small, those surrounding the glands radially arranged; lateral walls moderately thick, straight, unpitted; cuticle faintly granular. Stomata approximately 320 per sq. mm., absent above venules and in the vicinity of the glands; broadly elliptical, with an average size of 24 × 19μ and a range in the long axis of 19–26μ. Large stomata not developed. Peltate glands sparse, about 8 per sq. mm.; head oval, entire, composed of 8 cells; average diameter 39μ.

Upper Epidermis.—Cells small, lateral walls thick, straight and unpitted. Cuticle faintly granular. Glands sparse, about 8 per sq. mm.

Osmanthus Radula Hutch. New Caledonia.

Lower Epidermis.—Cells moderately large, radially arranged around the glands; cuticle granular. Stomata average 170 per sq. mm., widely spaced; absent from the

parenchyma over the veins and around the glands; elliptical, averaging 35 × 28μ, with a range in length of 30–37μ. Large stomata range from 44–67μ in length and have an average size of 51 × 33μ. Peltate glands very sparse, about 5 per sq. mm.; heads roughly circular, with an entire margin, divided into 8 irregular rays; average diameter is 40μ. Unicellular, thick-walled, sharply pointed hairs, about 80μ long, are scattered evenly over the surface.

Upper Epidermis.—Cells moderately large, with thick, straight, unpitted walls; cuticle granular. Glands very few, about 3 per sq. mm. Unicellular hairs sparse.

FOSSIL POLLEN OF OLEACOID TYPE.

Fossil pollen grains that show a close resemblance to grains of some recent members of the Oleineae occur in preparations made from ligneous clay at Maryvale, Victoria. Unfortunately this oleacoid type is not restricted to the family Oleaceae and cannot, therefore, be used as direct evidence in favour of the suggested oleaceous affinity of the fossil *Oleinites*. However, it is of interest and some significance to find such fossil pollen grains in beds deposited during the same period as those containing *Oleinites Willisii*. For this reason, therefore, it is recorded here as a new southern sporomorpha under the name *Tricolporites sphaerica.*

TRICOLPORITES SPHAERICA, n. sp. Plate ix, figs. 14, 15. Text-fig. 4.

Grains tricolporate, prolate-sphaeroidal to spherical, in equatorial view 25·5–29μ long and 25·5–29μ broad; furrows and pores conspicuous. Exine finely reticulate about 2μ thick, membrane over furrows smooth.

Locality.—State Electricity Commission Bore 155, 552 feet, Maryvale, Victoria.
Horizon.—Tertiary ? Oligocene-Miocene.
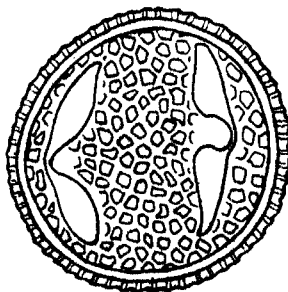
Text-fig. 4.—*Tricolporites sphaerica,* × 1,400.

Acetolysed pollen grains of some Australian species of Oleaceae have been compared with *Tricolporites sphaerica.* The latter are clearly distinct from grains of *Jasminum*, which apart from being larger, possess a distinctive beaded reticulum not unlike that of *Ligustrum* (Erdtman, 1943, Fig. 280). On the other hand, *Tricolporites sphaerica* agrees rather closely as regards size, shape and sculpture with pollen grains of such species of *Olea* as *O. paniculata* (Queensland), *O. Cunninghami* (New Zealand), *O. montana* (New Zealand) and *O. europaea.* In the living types, however, the furrows appear to be less sharply defined than in the fossil grains.

Pollen grains of *Notelaea,* e.g., *N. ligustrina* and *N. microcarpa,* although essentially similar to *Tricolporites sphaerica,* differ in being considerably smaller.

DIAGNOSES OF NEW GENUS AND SPECIES.
Genus OLEINITES, n. gen.

Leaves simple, petiolate, dorsiventral. Outer wall of upper epidermal cells thick, firm and highly cutinised; peltate hairs present on both surfaces; stomata of unequal size.

OLEINITES WILLISII, n. sp.

Leaves oblanceolate, tapering to a short petiole, 1–9 cm. long; apex retuse; margin thick, entire; with the exception of the midrib, quite veinless on both surfaces.

Horizon.—Tertiary ? Oligocene-Miocene.

Locality.—Open cut, Yallourn, Victoria.

Named in honour of Mr. J. H. Willis, B.Sc., of the National Herbarium of Victoria, who has shown considerable interest in the identification of this fossil type.

OLEINITES CRENULATA, n. sp.

Leaves broadly elliptic-lanceolate, narrowing at the base; apex obtuse to subacute, apparently retuse; margin crenulate, not conspicuously thickened; rugulose on both sides, more conspicuously so above, upper cuticle undulately striated.

Horizon.—Tertiary ? Oligocene-Miocene.

Locality.—Brown coal deposits, Moorlands, South Australia.

SUMMARY.

A new type, *Oleinites*, n. gen., is recorded from Tertiary brown coal deposits in south-eastern Australia.

Two species are distinguished.

Cuticular features which suggest affinity with the family Oleaceae are discussed.

Fossil pollen grains of oleacoid type are described under the sporomorpha *Tricolporites sphaerica*.

Cuticles of some recent species of *Olea, Notelaea, Osmanthus* and *Linociera* are briefly described.

BIBLIOGRAPHY.

BENTHAM, G., 1869.—*Flora Australiensis*, Vol. IV: 297-300.

COOKSON, I. C., 1946.—Pollens of *Nothofagus* from Tertiary Deposits in Australia. PROC. LINN. SOC. N.S.W., 71 (1-2) : 50.

ERDTMAN, G., 1943.—An Introduction to Pollen Analysis. Chronica Botanica Co., Waltham, Mass., U.S.A.

KNOBLAUCH, E., 1897.—Oleaceae-Naturl. Pflanzenfam. IV. Teil 2 : 1-19.

PRILLIEUX, ED., 1856.—De la Structure des Poils des Oléacées et des Jasminées. *Ann. Sci. Nat.,* (4) 5 : 5-14.

SOLEREDER, H., 1908.—Systematic Anatomy of the Dicotyledons (English Edition).

EXPLANATION OF PLATES VIII–X.

All the figures are from untouched negatives. C before a specimen number refers to the Cookson collection. Duplicate specimens will be deposited in the Department of Geology, British Museum.

Plate viii.

Fig. 1.—Sample of brown coal with thickly bedded cuticles of *Oleinites Willisii* from just beneath the overburden—open cut, Yallourn, Victoria. 5/6 nat. size (Nat. Mus. Vict., No. 14527).

Figs. 2, 3.—*O. Willisii.* Leaf cuticles viewed from above, showing range in size (C.203).

Fig. 4.—*O. Willisii.* Cuticle viewed from below, showing wide midrib and thickened margin, × 2 (C.200a).

Fig. 5.—*O. Willisii.* Distal region of upper cuticle, viewed from within, showing retuse apex and thick margin, × 2 (C.200b).

Fig. 6.—*Osmanthus Badula.* Apex of leaf from below, ×2.

Fig. 7.—*O. Willisii.* Portion of an upper cuticle, viewed from within, to show elevations in positions of peltate hairs, ×10.

Plate ix.

Fig. 8.—*O. Willisii.* Upper cuticle, ×110 (C.s. 52).

Fig. 9.—*O. Willisii.* Lower cuticle, ×78 (C.s. 53).

Fig. 10.—*O. Willisii.* Lower cuticle, ×110 (C.s. 53).

Fig. 11.—*O. Willisii.* Large stoma in region of midrib, ×150 (C.s. 54).

Fig. 12.—*Olea concolor.* Lower cuticle showing variations in size of stomata, ×150.

Fig. 13.—*Olea foveolata.* Lower cuticle showing linear arrangement of stomata, ×150.

Figs. 14, 15.—*Tricolporites sphaerica.* Pollen grain focused for furrows and sculpture of exine, respectively, ×1,400 (C.s. 55).

Plate x.

Fig. 16.—*Oleinites crenulata*. Portion of upper cuticle. Moorlands, South Australia. Nat. size (C.201).

Fig. 17.—*O. crenulata*. Apex of same specimen, × 4.

Figs. 18–21.—*O. crenulata*. Upper cuticles showing external features, × 2 (C.202).

Fig. 22.—*Olea paniculata*. Upper surface of portion of a dried leaf to show fine, reticulate venation, × 2.

Fig. 23.—*Oleinites crenulata*. Upper cuticle showing three peltate hairs and sinuate outlines of epidermal cells, × 150 (C.s. 48).

Fig. 24.—*O. crenulata*. Portion of upper cuticle showing peltate hair and undulating striations, × 250 (C.s. 49).

Fig. 25.—*O. crenulata*. Lower cuticle with large and small stomata, × 150 (C.s. 50).

Fig. 26.—*O. crenulata*. Lower cuticle showing deeply sinuate outlines of epidermal cells, × 150 (C.s. 51).

AUSTRALIAN BUPRESTIDAE: DESCRIPTION OF THREE NEW SPECIES OF THE GENUS *STIGMODERA*.

By C. Deuquet, B.Com.

(Three Text-figures.)

[Read 28th May, 1947.]

Of the three Stigmoderae described in the present paper, two are from the Stanthorpe district, in the highlands of southern Queensland, wherefrom a large number of brightly coloured Buprestidae have already been recorded.

The third is found in the New England district of New South Wales and also in southern Queensland, around Milmerran, where, surprisingly, several Western Australian species of Buprestidae and Cetoniidae have been taken, the finest being *Stigmodera pasroei* Saund., which until recently was thought to belong exclusively to Western Australia.

Stigmodera (Themognatha) gemmelli, n. sp. Fig. 1.

Oblong-oval. Head, pronotum and scutellum brilliant metallic green with golden reflections at sides of pronotum, legs green, antennae and tarsi bronzy-green. Elytra of ♂ testaceous with humeral ridges or epaulets and narrow lateral border extending from behind the shoulder swelling to the apex brownish and faintly sanguineous. Suture and apical teeth blue-green. Elytra of ♀ testaceous on upper part of disc and darker red past middle to the apex; narrow basal margin, external border and suture blue-green, extreme apex slightly tipped with green. Underside mostly shining metallic
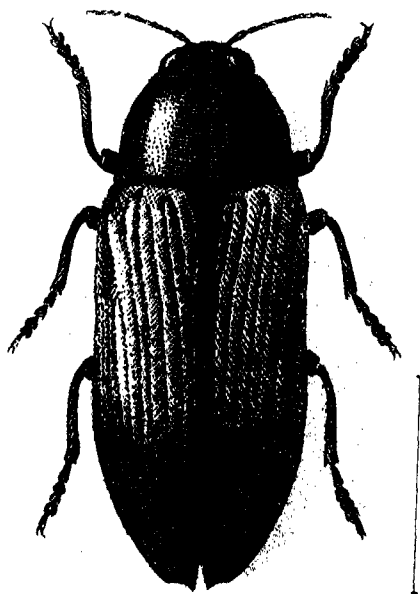
Fig. 1.—*Stigmodera (Themognatha) gemmelli*, n. sp. (Drawing by E. H. Zeck.)

P

green or greenish-bronze with the margins of abdominal segments yellow, the apical segment almost wholly yellow.

Head rugosely but irregularly punctate, rather strongly pubescent, slight vertical furrow.

Prothorax (♀, 10 × 6 mm.; ♂, 9 × 5 mm.) lightly convex, apex and base bisinuate, sides diverging rapidly for about half of their length then almost parallel to the base, the dorsal line smoothly indicated at the basal half by a shallow depression, disc finely and shallowly punctured, more coarsely and deeply so at sides, especially near the posterior angles. Scutellum cordate, impunctate, depressed in centre.

Elytra (♀, 21 × 11 mm.; ♂, 19 × 10 mm.) slightly wider than prothorax at base, lightly compressed just past shoulder then feebly widening and gradually narrowing to apex. Finely punctate, the punctures arranged in regular lines near the suture but very irregular near the shoulders and sides. Shoulders rather prominent. Suture slightly wider in ♀, particularly so on lower half. Apex widely truncate, each elytron feebly bidentate, the inner or sutural teeth the longer.

Underside shining, punctate and sparsely clothed with scattered long silvery hairs.
Dimensions: ♀, 30 × 11·5 mm.; ♂, 25 × 10 mm.

Habitat.—Stanthorpe, southern Queensland (A. Gemmell).

Four examples of this handsome and very localized species were examined. I am most grateful to Mr. A. Gemmell for a pair, and it affords me great pleasure to name it after this excellent naturalist.

Holotype (♀) and one paratype in Coll. Gemmell. Paratypes ♂ and ♀ in Coll. Deuquet.

STIGMODERA (CASTIARINA) RUTILA, n. sp.   Fig. 2.

Elongate, moderately convex. Head, antennae, pronotum, scutellum and legs bright bronze-green. Elytra uniformly blood-red except for the sombre bronze colour of the narrow basal margin and of the sutural line, the colour of the latter extending only to about 1 mm. from extreme apex, which is very faintly tipped with black.

Head punctured, lightly furrowed between the eyes.
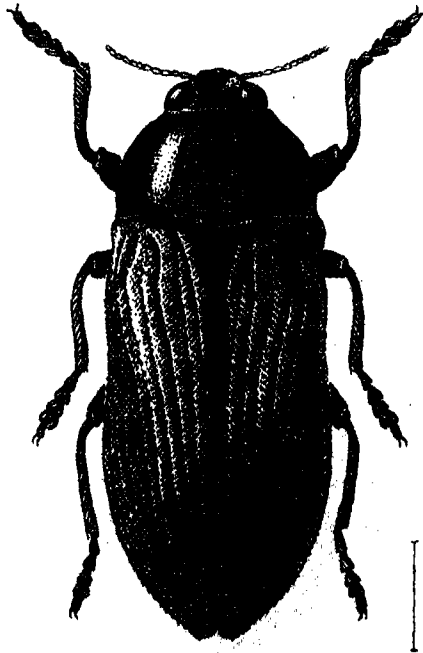
Fig. 2.—*Stigmodera (Castiarina) rutila*, n. sp.   (Drawing by E. H. Zeck.)

Prothorax closely, evenly and deeply punctate; anterior margin nearly straight and half the length of the base, sides rounded, base bisinuate. The dorsal line indicated at the base by a shallow median depression. Scutellum cordate with scattered irregular impressions.

Elytra of almost same width as prothorax at base, sides nearly straight on anterior two-thirds, thence narrowing arcuately to apex; surface punctured and striated, the slightly rounded interstices giving a smooth shiny appearance. Apex of each elytron sub-bidentate. Posterior margins finely denticulate. Underside evenly and finely punctate, lightly lanuginose.

Dimensions: 15 × 5·5 mm.

Habitat: Stanthorpe, southern Queensland (A. Gemmell).

This species whose habitat appears to be also strictly limited to the Stanthorpe district is a close ally of *S. indistincta* Saund., from which it differs (1) by the absence of fasciae on its elytra; (2) by the bright colour of its head, pronotum and appendages (the pronotum of the ♂ with its gold reflections being particularly brilliant), while these parts are nitid bronze in *S. indistincta*; (3) by its narrower width; and (4) by its more sharply attenuate form at apex.

Holotype (? ♀) and paratype in Coll. Gemmell. Paratypes ♂ and ♀ in Coll. Deuquet.

STIGMODERA (CASTIARINA) HUMILIS, n. sp. Fig. 3.

Ovate, widely oblong. Head, pronotum and scutellum dark bronze; clypeus, antennae, legs, tarsi and underside dark blue. Elytra uniformly orange-red, suture black.

Head finely punctured and fairly deeply furrowed between the eyes.

Prothorax moderately convex, widest at base; anterior margin almost straight and only slightly elevated; sides diverging in a slight curve till past the middle, feeble sinuation in middle leading to small dorsal fovea situated right above scutellum, the latter being only moderately depressed.

Elytra slightly wider behind shoulders, which are much wider than the base of the thorax and also past the middle; sides slightly raised, interstices closely punctate.
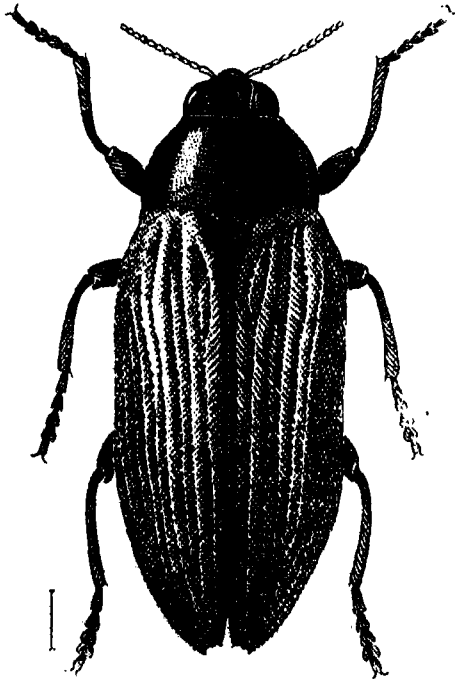
Fig. 3.—*Stigmodera (Castiarina) humilis*, n. sp. (Drawing by E. H. Zeck.)

Apex of each elytron with two small spines, the exterior one being slightly more prominent. Underside moderately punctate and sparsely clothed with white hairs, thickest at prosternum.

Dimensions: 7·5 × 3·5 mm.

Habitat: Southern Queensland and north-western New South Wales.

This species is not uncommon in the New England district of New South Wales and is found also in southern Queensland, and several specimens were kindly given to me recently by Mr. J. Macqueen of Milmerran, Queensland. In general appearance it is like *S. erythroptera* Boisd. and also resembles some examples of *S. balteata* Saund. which are occasionally found without sagittate subapical mark; but on closer view it can be easily separated from both. It differs from *S. erythroptera* by its lighter colour, smaller size, dark suture commencing at scutellum and extending almost but not quite to apex, smoother pronotum devoid of any fovea except the small shallow basal depression mentioned above, less rugose elytra and complete absence of apical or preapical mark. Also, the medial line of the pronotum, which is clearly defined in *S. erythroptera*, is almost indistinct in *S. humilis*. It differs from *S. balteata* by the redder colour of the elytra, suture commencing at scutellum, lateral margins of elytra more raised, and complete absence of apical or preapical mark connected or unconnected with suture.

Type (♂) in the Australian Museum, Sydney. Paratypes in Coll. Macqueen and in Coll. Deuquet. One paratype forwarded to British Museum of Natural History and one to the Queensland Museum, Brisbane.

THE CALCIUM CONTENT OF LEGUME ROOT NODULES.

By H. L. Jensen, Macleay Bacteriologist to the Society.

(From the Department of Bacteriology, University of Sydney.)

[Read 28th May, 1947.]

INTRODUCTION.

It is well known that the dry matter of leguminous plants is generally richer in calcium than that of non-legumes, and this has sometimes been taken as indicating that calcium is of specific importance for the process of symbiotic nitrogen fixation in the legumes, as well as for the non-symbiotic fixation by *Azotobacter*. Wilson (1940) has pointed out, however, that this high calcium content is also found in leguminous plants grown with combined nitrogen, a fact which suggests that the general metabolism of the legumes requires more calcium than that of other plants. Most of the available analytical figures refer to the aerial parts (stems and leaves) of legumes; there are few data concerning the roots, and the calcium content of the root nodules—the actual substrate of the process of nitrogen fixation—seems to have been determined quantitatively only in the more than sixty-year-old analyses of Troschke (1884, quoted by Czapek (1920) and Fred *et al.* (1932)), who found that the dry matter of roots and root nodules of lupins grown in water culture contained 0·46 and 0·75% of calcium,[*] respectively; the proportion of calcium in the ash of the two materials was not much different. Konishi and Tsuge (1936) made spectrographic determinations which were little more than qualitative, but which in most cases indicate a higher concentration of calcium in the nodules than in the roots of various legumes at successive stages of growth.

A number of pot experiments with lucerne and subterranean clover, of which a preliminary account has been given elsewhere (Jensen, 1946), yielded several samples of top, root and nodule materials which were analysed for calcium in order to find a possible clue to the question whether or not this element performs a specific function in the process of symbiotic nitrogen fixation as well as in *Azotobacter* (Burk and Lineweaver, 1931; Horner and Burk, 1934). Materials from a single experiment with field peas were also included.

EXPERIMENTAL.

Calcium was determined by Shapter's method as described by Piper (1942), with some minor modifications that were rendered necessary by the fact that only small amounts of nodule-substance, mostly 0·2–0·4 gm., were available for analysis. The volume of liquid in which the precipitation of calcium oxalate took place was reduced to about 40 ml., the precipitate was collected and washed by centrifugation instead of by filtration, and 0·05N potassium permanganate (1 ml. = 1 mgm. Ca) was used for the titration. In most cases there was not sufficient nodule-substance for duplicate determinations, but it was found that small known quantities of calcium could be recovered with a high degree of accuracy, as shown by the following figures:

Mgm. Ca taken					1·0	2·0	5·0	10·0
„ „ recovered—								
a.					1·02	2·05	4·96	9·95
b.					1·04	2·06	5·00	10·15

Firstly, a set of calcium determinations was made in nodules of subterranean clover and roots and nodules of lucerne, grown for 15 and 20 weeks, respectively, in acid sand adjusted to four ranges of reaction by addition of increasing amounts of calcium carbonate, besides a basal fertilizer-mixture containing adequate amounts of

---

[*] Or calcium oxide? The same figures are given by Fred *et al.* (1932) as "calcium" and by Czapek (1920) as "Kalk" (presumably CaO). Troschke's original paper has not been available to the author.

calcium as $CaSO_4$. The nodule-tissue in both plants showed a high degree of efficiency, fixing during the whole growth-period from 1,900 to 3,500 mgm. nitrogen per gm. dry nodule-substance in lucerne, and 720 to 1,200 mgm. in clover. The results are seen in Table 1, which shows that in both plants the calcium content of the nodules is of an order similar to that found by Troschke, and that there is no evidence of a clear-cut effect of the reaction. The lucerne roots are seen to contain only about one-half to one-third as much calcium as the nodules on the basis of dry matter, but the content of calcium in proportion to nitrogen is approximately the same in both plant organs, and actually higher in roots, at pH 7·6–7·7.

Another set of calcium determinations was made on top, root and nodule material of lucerne ("Giant Upright"), subterranean clover ("Mount Barker" and "Dwalganup"), and field peas. The source of nitrogen was atmospheric nitrogen unless otherwise stated. The results are seen in Table 2.

TABLE 1.

Calcium Content of Root Nodules of Lucerne and Subterranean Clover, and of Roots of Lucerne, grown in Sand of Different Reaction.

		0	0·01	0·04	0·4
	% $CaCO_3$ added to sand	0	0·01	0·04	0·4
Lucerne.	pH of sand initially	4·7–4·9	5·4–5·5	6·3–6·8	7·0–7·1
	" " " finally	4·3–4·5	4·7–4·1	6·9–7·2	7·6–7·7
	% Ca in nodules (dry matter)	0·95	0·73*	0·68	0·76
	" " " roots " "	0·27	0·27	0·24	0·37
	Ratio N/Ca in nodules	7·7	9·6	11·4	9·0
	" " " roots	8·6	9·2	9·9	5·1
Clover.	pH of sand initially	4·5	4·8–4·9	6·0–6·1	6·7
	" " " finally	4·1–4·3	4·5–4·7	6·2–6·4	7·6–7·7
	% Ca in nodules (dry matter)	0·46	0·58	0·75	0·55

* This figure is of doubtful accuracy because only a very small amount of substance was available for analysis.

TABLE 2.

Calcium Content and Ratio of Nitrogen to Calcium in Tops, Roots and Root Nodules of Leguminous Plants grown in Sand Culture.

Plant Species and Age.	Final pH of Sand.	% Ca in Dry Matter.			Ratio N/Ca.		
		Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.
1. Lucerne, 105 days	4·9–5·4	1·35	0·19	0·47	2·16	10·6	14·6
2. Lucerne, 88 days	5·1–5·6			0·55			13·1
3. Same, 102 days	6·0–6·1	1·49	0·24	0·35	2·11	10·2	20·5
4. Same, sand + $CaCO_3$, 88 d.	7·3–7·5			0·64			12·7
5. Same, 102 days	7·0–7·5	1·88	0·40	0·76	1·58	4·97	9·1
6. Sub. clover, 130 days	4·9–5·0	1·51	0·47	0·41	2·19	5·60	16·1
7. Same, combined nitrogen ($NaNO_3$+(NH_4)$_2SO_4$), 130 d.	4·8–5·3	1·18	0·43	0·34	2·48	6·49	19·3
8. Same, free N, sand + $CaCO_3$, 130 days	7·2–7·3	1·90		0·52	1·52		12·0
9. Sub. clover, 96 days	4·3–4·7	2·19	0·52	0·51	1·15	4·51	12·2
10. Same, combined nitrogen (NH_4NO_3), 96 days	4·7–4·8	1·96	0·54	0·41	1·39	5·16	15·1
11. Same, sand + $CaCO_3$, free nitrogen, 96 days	7·1–7·2	2·48	0·73	0·56	0·98	3·00	11·6
12. Same, combined nitrogen (NH_4NO_3), 96 days	7·3–7·5	2·63	0·84	0·54	1·02	3·17	13·3
13. Sub. clover ("Dwalganup"), 105 days	7·0–7·5	1·22	0·51	0·37	2·13	4·86	19·8
14. Field peas, 83 days	7·3–7·7	0·81	0·98	0·51	3·78	2·76	11·3

In all three plant species the calcium content of the nodules appears fairly constant and rarely departs much from 0·5%. In parallel experiments with acid and alkaline sand the calcium content is higher at alkaline reaction, but the difference is not very marked except in one case (lucerne after 102 days, Analyses Nos. 3 and 5). It is also noteworthy that provision of combined nitrogen does not cause any marked reduction in the calcium content of the small amount of nodule tissue that develops under these conditions. The calcium content of the clover roots is mostly similar to that of the nodules, but in the lucerne roots it is considerably lower (as in Table 1, and as found by Troschke in lupins). The pea tops appear somewhat low in calcium, but the tops of lucerne and clover show contents of 1·2–2·6% calcium, quite similar to figures quoted by Wilson (1940), slightly lower at acid reaction but not much influenced by the source of nitrogen. The nodules thus appear quite poor in calcium in comparison with the tops, and in proportion to the content of nitrogen the nodules actually contain less calcium than the other parts of the growing plant, as shown by the N/Ca ratios in Table 2.*

These results lend no support to the view that calcium is specifically needed for the process of symbiotic nitrogen fixation. (Neither can any such evidence be drawn from the fact that calcium stimulates nodule formation in soy bean seedlings at pH-values above 5·0, as shown by Albrecht (1933), since the number of nodules formed is not necessarily an index of the resulting nitrogen fixation; in this connection it is interesting to note the recent observation by Anderson and Thomas (1946) that molybdenum increases the nitrogen-fixing activity of the nodule-tissue, while actually reducing the number of nodules, a result which the present writer has been able to confirm.) It is possible, however, that calcium is needed in the tops and roots for other physiological purposes, such as neutralization of organic acids, synthesis of asparagin, activation of proteolytic enzymes, etc. (Nightingale, 1937; Wilson, 1940), in quantities which outweigh those that might be required for the functioning of the nodule-tissue, and this would presumably, like other plant tissues, require certain amounts of calcium apart from its possible importance for the specific process of nitrogen fixation. If calcium in this respect functions as a "trace element", even its concentration in the nodules appears relatively high. Assuming that fresh nodule-substance contains 25% dry matter and has a specific gravity of 1 (actually somewhat higher), a content of 0·5% calcium in dry matter corresponds to a concentration of 0·125 mgm. calcium per cubic centimetre of nodule-tissue, or roughly 3×10^{-3} molar. This is considerably more than the quantities required by *Azotobacter*, in which Burk and Lineweaver (1931) found that a supply of 25–50 mgm. calcium per litre, or 0·6–1·2 × 10^{-3} molar, was necessary for normal growth with free nitrogen, while Burk and Horner (1934) later found that concentrations of 0·02–0·04 × 10^{-3} molar were sufficient for half-optimal rate of fixation (it may be noted, however, that this was probably under conditions of partial molybdenum-deficiency).

Upon the whole it seems that the question of the essentiality of calcium for symbiotic nitrogen fixation cannot be finally answered until it becomes possible to make the root nodule bacteria fix nitrogen *in vitro*.

SUMMARY.

Effective root nodules of lucerne, subterranean clover and field peas, grown in sand culture, contained from 0·34 to 0·95% calcium in dry matter, compared with 0·19 to 0·98% in the roots and 0·8 to 2·6% in the tops. Although usually higher at alkaline reaction, the calcium content of the nodules was mostly not strongly influenced by the reaction of the sand or the supply of combined nitrogen to the plants. The nodules contained less calcium in proportion to nitrogen than did either the roots or

* The seeds from which the plants were grown proved even poorer in calcium, both absolutely and in proportion to nitrogen, as shown by the following analytical figures:

	Lucerne.	Sub. Clover. ("Dwalganup").	Pea.
% Ca in dry matter	0·15	0·20	0·14
Ratio N/Ca	40·7	25·5	22·1

the tops. The results give no evidence that calcium is needed specifically for the process of nitrogen fixation, but do not allow any final conclusion in this respect.

REFERENCES.

ALBRECHT, W. A., 1933.—Inoculation of Legumes as related to Soil Acidity. *J. Amer. Soc. Agron.*, 25 : 512-522.

ANDERSON, A. J., and THOMAS, MARGARET P., 1946.—Plant Responses to Molybdenum as a Fertilizer. 1. Molybdenum and Symbiotic Nitrogen Fixation. *Coun. Sci. Industr. Res.*, Melbourne, Bull. No. 198.

BURK, D., and LINEWEAVER, H., 1931.—The Influence of Calcium and Strontium upon the Catalysis of Nitrogen Fixation by *Azotobacter*. *Arch. Mikrobiol.*, 2 : 155-186.

CZAPEK, F., 1920.—Biochemie der Pflanzen. Vol. 2, IV : Die Mineralstoffe im pflanzlichen Stoffwechsel. Jena.

FRED, E. B., BALDWIN, I. L., and McCOY, ELIZABETH, 1932.—Root Nodule Bacteria and Leguminous Plants. Madison.

HORNER, K., and BURK, D., 1934.—Magnesium, Calcium and Iron Requirements for Growth of *Azotobacter* in Free and Fixed Nitrogen. *J. Agric. Res.*, 48 : 981-995.

JENSEN, H. L., 1946.—The Nitrogen-fixing Activity of Legume Root Nodules. *Aust. J. Sci.*, 9 : 118.

KONISHI, K., and TSUGE, T., 1936.—On the Mineral Matters of Certain Leguminous Crops. *Mem. Coll. Agric., Kyoto Imp. Univ.*, No. 37.

NIGHTINGALE, G. T., 1937.—The Nitrogen Nutrition of Green Plants. *Bot. Rev.*, 3 : 85-174.

PIPER, C. S., 1942.—Soil and Plant Analysis. Adelaide.

WILSON, P. W., 1940.—The Biochemistry of Symbiotic Nitrogen Fixation. Madison.

FOSSIL FUNGI FROM TERTIARY DEPOSITS IN THE SOUTHERN HEMISPHERE. PART I.

By Isabel C. Cookson, D.Sc., Department of Botany, University of Melbourne.
(*Communicated by Dr. W. R. Browne.*)

(Plates xi- xiv.)

[Read 30th July, 1947.]

INTRODUCTION.

During the examination of acetolysed residues prepared primarily for the purpose of Tertiary pollen and spore analyses, detached shield-shaped fruit-bodies with radial structure were observed. They showed a close resemblance to the ascomata or thyriothecia of the Microthyriaceae.

Subsequent examination of mummified leaves of *Oleinites Willisii* Cookson (1947) revealed additional closely-related types and gave further information regarding one of the forms mentioned above.

In this paper the more clearly defined fungi, discovered by these means, will be described. The remaining forms, when better understood, will form the subject of a second paper.

A few fossil fungi of suggested microthyriaceous affinities have been identified in European Tertiary deposits. While the identity of some of these appears to be somewhat uncertain, such excellently preserved ascomata as those of *Phragmothyrites eocaenica* Edw. from Mull in Scotland (Edwards, 1922) leave no doubt of the existence there of the family Microthyriaceae in early Tertiary times.

The demonstration, as the result of the present investigation, of this family in rocks of the Southern Hemisphere is therefore not surprising. However, some stratigraphical and palaeoecological significance attaches to this discovery. Of mycological interest is the record of two allied families, hitherto unrepresented by fossil species.

SOURCE AND AGE OF FOSSILS.

The deposits in which the fossil fungi are contained occur in places as widely separated as Kerguelen Archipelago and New Zealand.

For the material from Kerguelen Archipelago, I am indebted to Sir Douglas Mawson, who kindly made available for examination specimens collected there by the B.A.N.Z. Antarctic Research Expedition. For samples of coal from New Zealand, as well as for information concerning them, I wish to thank Mr. W. F. Harris and Mr. Martin Te Punga. The Australian localities are, in the main, those discussed in a previous paper (Cookson, 1946). In no instance can an exact statement be made regarding the age of the beds in question. The generally accepted approximations will be given below.

Kerguelen Archipelago.

Kerguelen Island, near Port Jeanne d'Arc. Carbonaceous sandstone associated with lignite. Specimen No. C.250. Late Oligocene (Mawson, 1933).

Australia.

Yallourn, Victoria. Leaves of *Oleinites Willisii*, from State Electricity Commission's open cut. ? Oligocene-Miocene.

Hazelwood, south of Maryvale, Victoria. Leaves of *O. Willisii*, S.E.C. Bore 28 at 150 feet. Oligocene-Miocene.

Q

Traralgon, east of Yallourn. Ligneous clay from S.E.C. Bore 23 at 497 to 500 feet. Oligocene-Miocene.

Sentinel Rock, Aire Coast, Victoria. Post-Middle-Miocene (Singleton, 1941, p. 74).

Kiandra (New Chum Hill), New South Wales. Soft lignitic shale, 135 feet below base of basalt. Dulhunty collection, coal sample 103. Oligocene-Miocene.

Vegetable Creek, New South Wales. Mudstone. Oligocene-Miocene.

New Zealand.

Ohai, Birchwood Mine. Highly cleaved black coal, Geological Survey of New Zealand coal sample 243. ? Oligocene.

SYSTEMATIC POSITION OF FOSSILS.

All the fossil fungi to be described below are members of the order Hemisphaeriales Theiss. This order is typified by the dimidiate form of the fruit-body or ascoma as well as by the frequency of its radial construction.

Three of the six families of the order (Ainsworth and Bisby, 1943) are represented in the present collection of types. The majority of these have flat, superficial ascomata with radial structure and fall within the limits of the Microthyriaceae Sacc. One form, on account of its thalloid nature, is clearly a member of the Trichopeltaceae Theiss. Another example with plectenchymatous structure represents the Micropeltaceae Clements and Shear.

Ascospores, the characters of which provide a valuable distinction between the living genera of these families, have not been detected either within or in close association with the fossil ascomata. Moreover, the treatment to which these bodies have been subjected implies loss of such additional diagnostic characters as the form of the asci and presence or absence of paraphyses. Detailed systematic determinations and the establishment of close affinity between living and fossil genera are therefore not possible, although, in some cases, there may be striking morphological agreement between them. The genus *Phragmothyrites*, described by Edwards as having phragmo-septate spores, is, for the same reason, not open for use.

For convenience in future reference, new genera, based on external morphological characters, are here created for the reception of these southern Tertiary fungi. In order to minimize their number, generic descriptions are made as broad as possible; distinctions, which amongst living species would certainly be considered of generic rank, being regarded as only of a specific value.

DESCRIPTIONS OF FOSSIL FUNGI.

1. Family MICROTHYRIACEAE Sacc.

The grouping of the living genera of this family into two sub-families is based upon the presence or absence of a mycelium when the ascomata are mature (Stevens and Ryan, 1939). Those genera in which the mycelium is evanescent are placed in the sub-family Microthyreae Sacc. and Syd., those in which a free mycelium persists constituting the sub-family Asterineae Sacc. and Syd.

This character is a difficult one to determine when ascomata are unrelated to leaf cuticles. In such cases the apparent absence of mycelial hyphae might be a natural feature or one due either to faulty preservation or to the mode of treatment of the matrix in which the fossils occur. In cuticular preparations this feature can be relied upon with greater confidence, and it is information gained from such material that allows the adoption of the following classification.

Sub-family MICROTHYREAE.

Genus NOTOTHYRITES, n. gen.

Ascomata without free mycelium, superficial, rounded, radiate, ostiolate. Ostiole prominent, bordered by three to five layers of dark brown, thick-walled cells. Ascospores unknown.

NOTOTHYRITES SETIFERUS, n. sp.   Plate xi, figs. 1-6.

Ascomata flattened-hemispherical with a somewhat sinuous outline, 70-135μ in diameter, solitary, composed of radiating hyphae connected throughout their whole length.   Cells approximately 4-13μ long and 4-10μ thick, frequently becoming more elongated towards the periphery. Cell walls of the majority of cells thin but the outer walls of the peripheral layer frequently strongly thickened to form the firm, entire margin of the ascoma (Plate xi, figs. 3, 4).   The ostiole is well defined, distinctly elevated and either centrally or slightly excentrically placed. It is 10-16μ in diameter and bordered by three or four layers of dark brown, thick-walled cubical cells.   The border is cylindrical and some of the cells bear setae, the number approximating to eight.   The setae are short, about 13μ, non-septate, and their walls are thick and brown below, thinning towards lighter, bluntly-pointed apices (Plate xi, fig. 4).

Type Localities: Kerguelen Island, and Kiandra, New South Wales.

From the Vegetable Creek matrix, as well as from the type localities, ascomata, similar in other respects to those regarded as being typical of N. setiferus, have been observed which appear to be glabrous. The possibility suggests itself that this condition may have resulted from the destruction of setae either during fossilization or the chemical treatment to which the ascomata were subjected. This point of view is supported by the considerable numerical variability of the setae.   It seems highly improbable, for example, that the observed range of from one to eight (Plate xi, figs. 1-3) is a natural one. For the present, therefore, these doubtful examples will be included in N. setiferus.

In its typical form A. setiferus strongly resembles the living species Chaetothyriopsis panamensis Stevens and Dorman (Stevens, 1927) from Panama-Darien, the border of the ostiole and the development of setae being features common to both. The setae of C. panamensis, however, are considerably longer and apparently less numerous than are those of N. setiferus.

NOTOTHYRITES AIRENSIS, n. sp.   Plate xi, fig. 7.

Ascomata flattened-hemispherical, glabrous, 90-160μ in diameter, composed of radiating hyphae united along their whole length, cells thin walled, cubical to rectangular, 2·5-5·5μ thick and 3 to 13μ long. Margin thin, entire. Ostiole well defined, 8μ in diameter, surmounting a prominently-raised, dark brown, conical border composed of four or five layers of thick-walled cells, the base of which is 29·5μ in diameter.

Sentinel Rock beds, Aire Coast, Victoria.

This description is based on five specimens from the Sentinel Rock beds, the characters in which they appear to differ from N. setiferus being evident in all of them.   The main distinctions are the narrower ostiole, the conical form and degree of prominence of its border and the absence of setae. The finer texture of the ascomal membranes becomes evident when the specimen illustrated in Plate xi, figure 7, is compared with specimens of N. setiferus shown in Plate xi, figures 3 and 5.

A small piece of upper epidermis of Oleinites Willisii from Yallourn (C.s. 38) shows two ascomata of Notothyrites in situ.   These seem closer to N. airensis than to N. setiferus and are therefore provisionally placed in that species. No hyphae accompany these ascomata, so that the opinion formed from a study of detached examples that the mycelium of Notothyrites was evanescent is substantiated by them.

Sub-family ASTERINEAE.

(A). ASCOMATA ROUND.

Genus ASTEROTHYRITES, n. gen.

Mycelium superficial, persistent. Ascomata round, flat, radiate. Ascospores unknown.

ASTEROTHYRITES SINUATUS, n. sp.   Plate xii, fig. 8.

Amphigenous; mycelium fine, hyphae brown, non-hyphopodiate, about 2·5μ thick, somewhat flexuous. Ascomata scattered, brown, astomate, 74-106μ in diameter, composed of rather slender, straight or slightly flexuous radiating hyphae; central cells small,

hexagonal or cubical, peripheral cells cubical to rectangular thin walled, approximately $2 \cdot 5$–$3 \cdot 5 \mu$ thick and $2 \cdot 5$–$3 \cdot 5 \mu$ long. Margin of ascoma entire and sinuous; dehiscence by means of a stellate fissure.

On leaves of *Oleinites Willisii* from Yallourn and Hazelwood, Victoria.

ASTEROTHYRITES DELICATISSIMUS, n. sp.   Plate xii, fig. 9.

Amphigenous; mycelium fine, brown, non-hyphopodiate, hyphae about 2μ thick. Ascomata scattered, brown, astomate, 66–106μ in diameter, composed of thin, straight, radiating hyphae joined throughout their whole length. Cells thin walled, rectangular, $2 \cdot 0$–$2 \cdot 5 \mu$ thick. Margin delicate, not fimbriate.

On leaves of *Oleinites Willisii* from Yallourn, Victoria.

This species is readily distinguished by the fine construction of the ascomata and the fact that the marginal and peripheral layers are seldom preserved.

ASTEROTHYRITES MINUTUS, n. sp.   Plate xii, fig. 10.

Amphigenous; mycelium sparse, brown, non-hyphopodiate, about 2–$2 \cdot 5 \mu$ thick. Ascomata scattered, small, 47–80μ in diameter, composed of united hyphae which radiate from a single central cubical or hexagonal cell; cells almost cubical to rectangular, about 3μ thick, rather thick walled; margin thin, not fimbriate.

On leaves of *Oleinites Willisii* from Yallourn, Victoria.

In lignitic shale, Kiandra, New South Wales.

ASTEROTHYRITES OSTIOLATUS, n. sp.   Plate xii, fig. 11.

Epiphyllous; mycelium sparse, brown, hyphae about $2 \cdot 6 \mu$ thick. Ascoma stomate, flattened, 106μ in diameter, composed of somewhat tortuous hyphae; cells cubical or rectangular, 2–5μ thick, thick walled; margin uneven and slightly fimbriate; stoma round, 13μ in diameter, formed by the breaking down of the central cells.

On a leaf of *Oleinites Willisii* from Yallourn, Victoria.

The limits of this species are less clearly defined than are those of the three preceding species of *Asterothyrites*. One reason is the fact that the single specimen on which it is based is not perfect, the margin being incomplete in several places. Nevertheless, it is clearly distinct from the previous types and thus warrants description.

Several fragments of ostiolate ascomata from Sentinel Rock beds suggest comparison with the Yallourn species. They are recorded as doubtful additional examples of *A. ostiolatus*.

(B). ASCOMATA LINEAR.
Genus EUTHYTHYRITES, n. gen.

Mycelium superficial; ascomata linear, radiate. Characters of spores unknown.

EUTHYTHYRITES OLEINITIS, n. sp.   Plate xiii, figs. 12, 13.

Amphigenous; ascomata scattered, brown, 226–540μ × 90–160μ, elliptical, forked or triradiate with rounded ends, dehiscing by a longitudinal slit along the length of the ascoma; cells cubical to rectangular, $5 \cdot 0$–$10 \cdot 5 \mu$ long and $2 \cdot 5$–$5 \cdot 0 \mu$ thick, rather thick walled. Mycelial hyphae non-hyphopodiate, brown, 3–4μ thick, straight, radiating from the marginal cells of the ascoma.

On leaves of *Oleinites Willisii* from Yallourn and Hazelwood, Victoria.

It is of interest to note that two living species with linear ascomata and a persistent mycelium have been recorded on extra-Australian oleaceous leaves. They are *Aulographum hederae* Lib. var. *oleae* Sacc. and *Lembosiopsis oleae* (Tracy and Earle) Theiss; both agree with *Euthythyrites oleinitis* in having a non-hyphopodiate mycelium.

MICROTHYRIACEAE INCERTAE SEDIS.
Genus MICROTHYRIACITES, n. gen.

Ascomata radiate and dimidiate. Information regarding the presence of a free mycelium either uncertain or wanting; ascospores unknown.

MICROTHYRIACITES FIMBRIATUS, n. sp. Plate xiii, fig. 17.

Ascomata round, flattened, astomate, brown, sometimes confluent, 74–133μ in diameter, composed of hyphae which radiate from a large, thick-walled, hexagonal, central cell 8–13μ in diameter. The more centrally-placed cells thick walled and almost cubical, peripheral cells rectangular, 2·6–5μ thick, with thinner walls. Margin slightly fimbriate.

In ligneous clay, Traralgon Bore 23,500 feet.

MICROTHYRIACITES GRANDIS, n. sp. Plate xiv, figs. 20, 21.

Ascoma large, round, flattened, astomate, 280μ in diameter, composed of stout, thick-walled, completely united hyphae which radiate from a central group of hexagonal cells. Cells 6·6–10·0μ thick.

In coal, Birchwood Mine, Ohai, New Zealand.

My object in describing this single imperfectly preserved specimen is to provide evidence of the occurrence of the Microthyriaceae in New Zealand during the Tertiary period. It is to be hoped that additional specimens will give the information regarding the margin necessary to complete the specific description.

The specimen from Traralgon, Victoria, illustrated in Plate xiv, fig. 21, although considerably smaller (186μ in diameter), is compared with *M. grandis* on account of its similar construction. Unlike the type specimen, the margin which is thick and non-fimbriate is preserved.

MICROTHYRIACITES sp. Plate xiii, figs. 18, 19.

Ascomata astomate, flattened-hemispherical, brown, about 103–106μ in diameter, composed of united radiating hyphae, central cells hexagonal, peripheral cells cubical to rectangular, 5·0–8·5μ thick, thin walled. Margin not fimbriate.

On under epidermis of *Oleinites Willisii*, Yallourn, Victoria.

On an unidentifiable fragment of cuticle in coal from Birchwood Mine, Ohai, New Zealand.

These ascomata were found in insufficient numbers for specific assignment. It is not clear that they represent mature ascomata, and it is possible that they are developmental stages of a large species such as *M. grandis*. In both specimens hyphae were observed on the cuticular surface, but their association with the ascomata in question is by no means certain.

2. Family TRICHOPELTACEAE Theiss.

Members of this family are distinguished from the Microthyriaceae by the lateral union of mycelial hyphae to form a one-layered, radially-constructed thallus. This may be irregularly strap-shaped as in the sub-family Trichopeltineae Theiss. or more or less circular in outline as in the sub-family Brefeldineae Theiss. (Theissen, 1914).

No fossil representative of the Brefeldineae has hitherto been recorded, nor has this type been observed during the present investigation; but the branched ribbon-like thalli typical of the Trichopeltineae occur frequently and in considerable numbers on leaves of *Oleinites Willisii*.

As was the case with the fossil Microthyriaceae, the absence of information regarding ascospore characters prevents assignment of this thalloid form to any one of the living species of the Trichopeltineae. For this reason, in naming it, I propose to combine the name of the sub-family with the suffix -ites.

Genus TRICHOPELTINITES, n. gen.

Thallus that of the Trichopeltineae. Ascomata developed as thickened areas of the thallus and dehiscing by an irregular ostiole as in *Trichopeltis* Theiss. (Stevens, 1925). Ascospores unknown.

TRICHOPELTINITES PULCHER, n. sp. Plate xiv, figs. 22, 23.

Thallus epiphyllous, dark brown, from 18–150μ in width, frequently narrow-elongate with many lobes and some branches, sometimes broader and more leaf-like in form.

Cells 3–7μ broad and 5–8μ long with straight, firm walls. Ascomata 72–90μ in diameter, darker brown than thallus, opening by an irregular fissure.

On upper surface of leaves of *Oleinites Willisii* from Yallourn and Hazelwood, Victoria.

T. pulcher is strikingly similar to *Trichopeltis reptans* Speg. and undoubtedly is closely allied to, if not identical with, that species.

3. Family MICROPELTACEAE Clements and Shear.

This family is distinguished from the Microthyriaceae and Trichopeltaceae by the non-radiate construction of the flattened ascomata. The structure of the ascomal membrane or "scutellum" varies within the family and provides the basis for its subdivision into three sub-families (Stevens and Manter, 1925). Only one of these, namely, the Plochmopeltineae Theiss., is represented in the present collection. This sub-family contains a small number of living species all of which are characterized by the sinuous plectenchymic structure of the "scutellum".

Genus PLOCHMOPELTINITES, n. gen.

Fossil ascomata of dimidiate form with ascomal membranes of sinuous plectenchyma. Ascospore characters unknown.

PLOCHMOPELTINITES MASONI, n. sp.   Plate xiii, figs. 14, 15.

Ascomata superficial rounded, brown, glabrous, ostiolate 106–200μ in diameter with an entire, irregularly sinuate margin. Covering membranes prosenchymatous composed of slender, wavy hyphae from 2–5μ thick, those of the central region being, sometimes, thicker walled than those of the periphery. Straighter branches may become free and extend beyond the limits of the ascoma. Ostiole 9–25μ in diameter surrounded by a dense, slightly-raised border.

In carbonaceous sandstone, Kerguelen Island.

On unidentifiable fragments of cuticle in lignitic shale, Kiandra, New South Wales.

In ligneous clay, Bore 23, at 500 feet Traralgon, Victoria.

I have pleasure in naming this species in honour of Mr. E. W. Mason, M.A., who gave helpful advice concerning its taxonomy.

CONCLUSION.

The living members of the families just discussed live superficially on leaves, and some of them may be considered as components of "sooty-mould" associations. The Microthyriaceae are believed to be ecto-parasitic "sooty-moulds" (Fisher, 1939, p. 401). The Trichopeltaceae, on the other hand, are considered by Fraser (1936) to be "true saprophytes living on 'honey dew' like members of the Capnodiaceae". The mode of nutrition of the Micropeltaceae has not been studied in any detail and these "fly speck" fungi have not been identified as endemic components of "sooty-mould" communities.

Such fungi are most abundant in warm-temperate and tropical zones, but their incidence in such areas appears to be due to high humidity rather than to high temperatures. Edwards (1922, p. 71) reports Arnaud as having asserted that "asterinoid" fungi are confined to parts of the globe with more than one metre of rainfall per annum.

In Australia a few species of Microthyriaceae have been recorded from Queensland and Victoria (Cooke, 1899), that is, from tropical and cool-temperate latitudes. Their "hosts", however, inhabit either rain-forest areas or moist mountain gullies, as in southern Victoria.

The same applies to the Trichopeltaceae. Fraser (loc. cit.) has recorded three species from rain-forest trees in New South Wales, and Theissen identified *Trichopeltis reptans* on leaves of *Drimys lanceolata* (Poir.) Baill. (*aromatica* F.v.M.) from Tasmania. Dr. Eileen Fisher in 1945 observed, but did not record, Trichopeltaceae on leaves of *Nothofagus Cunninghami* (Hook.) Oerst from fern gullies near Marysville, Victoria.

The family Micropeltaceae as a whole has not been investigated by Australian mycologists and its absence from our fungal flora is probably more apparent than real. The sub-family Plochmopeltineae, with which this investigation is concerned, has not been recorded for Australia. Its few species are restricted to such tropical regions as British Guiana, Hawaii, Ceylon, India and Africa. The fossil genus *Plochmopeltinites*, by its occurrence in southern latitudes at Kerguelen Island and in southern Australia, indicates a far wider distribution for this sub-family during the Tertiary epoch.

From experimental data concerning the temperature and moisture requirements of certain "sooty-moulds" (Fisher, loc. cit.), it seems safe to assume that the humidity in the regions where these deposits were accumulating was at least as great as it is now in situations favourable to the growth of such fungi. The occurrence of *Microthyriacites* in New Zealand coals of approximately the same age as the deposits in Australia and Kerguelen Island suggests that similar climatic conditions prevailed in these widely-spaced sub-antarctic regions.

Temperature does not seem to be a major factor in determining the presence or absence of these species. Nevertheless, the fact that the Plochmopeltineae have not, as yet, been found outside the tropics provokes the thought that the temperature in southern latitudes during the Tertiary epoch may have been higher than it is at present.

The occurrence of several of these species on the leaf referred to as *Oleinites Willisii* requires brief mention. This particular leaf has characteristic peltate hairs on both surfaces. If these hairs were glandular in character, the so-frequent occurrence and often copious growth of fungi on their surfaces might be explained.

Perfectly preserved developmental stages in ascoma formation have often been met with but no attempt has been made, as yet, to relate these to any of the species just dealt with.

The photographic illustrations of this paper were prepared by Mr. E. Matthaei, of the Faculty Workshop of the University of Melbourne; their cost was generously defrayed by the State Electricity Commission of Victoria.

SUMMARY.

Eleven new fossil species belonging to the order Hemisphaeriales of the Ascomycetes have been described.

Three families of the order are represented, namely, the Microthyriaceae, Trichopeltaceae and Micropeltaceae.

These fungi were discovered in Tertiary deposits of Kerguelen Archipelago, Australia and New Zealand.

The palaeoecological significance of this occurrence is discussed.

BIBLIOGRAPHY.

AINSWORTH, C., and BISBY, G. R., 1943.—A Dictionary of Fungi.

COOKE, M. C., 1892.—Handbook of Australian Fungi.

COOKSON, I. C., 1946.—Pollens of *Nothofagus* Blume from Tertiary Deposits in Australia. PROC. LINN. SOC. N.S.W., 71 : 49-63.

————, 1947.—On Fossil Leaves (Oleaceae) and a New Type of Fossil Pollen Grain from Australian Brown Coal Deposits. PROC. LINN. SOC. N.S.W., 72 : 183-197.

DOIDGE, ETHEL M., 1920.—South African Microthyriaceae. *Trans. Roy. Soc. S. Afr.*, 8 : 235-281.

EDWARDS, W. N., 1922.—An Eocene Microthyriaceous Fungus from Mull, Scotland. *Trans. Brit. Mycol. Soc.*, 8 : 66-72.

FISHER, E. E., 1939.—A Study of Australian "Sooty Moulds". *Ann. Bot.*, 3 : 399-426.

FRASER, L., 1936.—Notes on the Occurrence of the Trichopeltaceae and Atichiaceae in New South Wales. PROC. LINN. SOC. N.S.W., 61 : 277-279.

MAWSON, SIR D., 1933.—The Geology and Glaciation of Some Islands of the Southern Ocean, etc. *Proc. Geol. Soc. Lond.*, Abstracts, 19th May, 1933.

NATHORST, A. G., 1915.—Tertiäre Pflanzenreste aus Ellesmere-Land. Rep. 2nd Norwegian Arctic Expedition in "Fram", 1898-1902, No. 35.

RYAN, RUTH W., and STEVENS, F. L., 1925.—Microthyriaceae in Hawaiian Fungi. *Bernice P. Bishop Mus. Bull.* No. 19 : 66-78.

SINGLETON, F. A., 1941.—The Tertiary Geology of Australia. *Proc. Roy. Soc. Vict.*, 53 : 1-125.

Stevens, F. L., 1925.—Trichopeltaceae in Hawaiian Fungi. *Bernice P. Bishop Mus.* Bull. No. 19 : 78-86.
———, 1927.—New Tropical Fungi. *Mycologia,* 19 (5) : 231-238.
Stevens, F. L., and Manter, H. W., 1925.—The Hemisphaeriaceae of British Guiana and Trinidad. *Bot. Gaz.,* 79 : 265-294.
———, and Ryan, Sister Mary Hilaire, 1939.—The Microthyriaceae. *Ill. Biol. Monogr.,* Vol. 17.
Theissen, F., 1913.—Hemisphaeriales. *Annales Mycologici,* Vol. 11 : 468-469.
———, 1914.—Trichopeltaceae n. fam. Hemisphaerialium. *Centralbl. für Bakter. und Parasitank.,* (2) 39 : 625-640.

EXPLANATION OF PLATES XI-XIV.

All the figures are from untouched negatives. C.s. before a specimen number refers to the Cookson Slide Collection. Duplicate slides, where possible, will be deposited at the Imperial Mycological Institute, Kew, England.

Plate xi.

Fig. 1.—*Notothyrites setiferus.* An ascoma with two setae viewed from above. Kiandra, New South Wales. × 520. (C.s. 26.)

Fig. 2.—*N. setiferus.* Covering membrane of an ascoma showing seta. Kiandra, New South Wales. × 520. (C.s. 27.)

Fig. 3.—*N. setiferus.* Ascoma, with setae, folded back and viewed from the side. Kerguelen Island. × 520. (C.s. 28.)

Fig. 4.—*N. setiferus.* Portion of an ascoma showing two setae and thick margin. Kerguelen Island. × 520. (C.s. 29.)

Fig. 5.—*N. setiferus.* Covering membrane of an ascoma viewed from beneath. Kerguelen Island. × 520. (C.s. 30.)

Fig. 6.—*N. setiferus.* An ascoma viewed from beneath. Vegetable Creek, New South Wales. × 520. (C.s. 31.)

Fig. 7.—*N. atrensis.* An ascoma viewed from above. Sentinel Rock beds, Victoria. × 520. (C.s. 32.)

Plate xii.

Fig. 8.—*Asterothyrites sinuatus.* An ascoma on upper epidermis of *Oleinites Willisii.* Yallourn, Victoria. × 520. (C.s. 33.)

Fig. 9.—*Asterothyrites delicatissimus.* An ascoma showing disconnected portions of the margin, on the upper epidermis of *O. Willisii.* Yallourn, Victoria. × 520. (C.s. 34.)

Fig. 10.—*Asterothyrites minutus.* An ascoma on upper epidermis of *O. Willisii.* Yallourn, Victoria. × 520. (C.s. 35.)

Fig. 11.—*Asterothyrites ostiolatus.* An ascoma on upper epidermis of *O. Willisii.* Yallourn, Victoria. × 520. (C.s. 36.)

Fig. 12.—*Euthythyrites oleinitis.* A small ascoma on upper epidermis of *O. Willisii.* Yallourn, Victoria. × 175. (C.s. 37.)

Fig. 13.—*E. oleinitis.* A large ascoma, showing origin of mycelial hyphae, on upper epidermis of *O. Willisii.* Yallourn, Victoria. × 170. (C.s. 38.)

Plate xiii.

Fig. 14.—*Plochmopeltinites Masoni.* "Scutellum" on fragment of cuticle. Bore 23, 497-500 feet, Traralgon, Victoria. × 520. (C.s. 39.)

Fig. 15.—*P. Masoni.* Portion of another ascoma. Kiandra, New South Wales. × 520. (C.s. 40.)

Fig. 16.—*Microthyriacites fimbriatus.* A group of ascomata showing confluent habit and fimbriate margin. Bore 23, 497-500 feet, Traralgon, Victoria. × 520. (C.s. 41.)

Fig. 17.—*M. fimbriatus.* Another example showing fimbriate margin. Bore 23, 497-500 feet, Traralgon, Victoria. × 520. (C.s. 42.)

Fig. 18.—*Microthyriacites* sp. An ascoma on leaf of *O. Willisii.* Yallourn, Victoria. × 520. (C.s. 43.)

Fig. 19.—C.f. *Microthyriacites* sp. An ascoma on fragment of cuticle. C.S. 243, Birchwood Mine, Ohai, New Zealand. × 520. (C.s. 44.)

Plate xiv.

Fig. 20.—*Microthyriacites grandis.* An ascoma. C.S. 243, Birchwood Mine, Ohai, New Zealand. × 260. (C.s. 45.)

Fig. 21.—C.f. *Microthyriacites grandis.* An ascoma. Bore 23, 499-500 feet, Traralgon, Victoria. × 260. (C.s. 46.)

Fig. 22.—*Trichopeltinites pulcher.* Thallus on upper epidermis of *O. Willisii,* Yallourn, Victoria. × 260. (C.s. 47.)

Fig. 23.—*T. pulcher.* Branched thallus showing an ascoma. × 260. (C.s. 37.)

STUDIES ON THE ECONOMIC BIOLOGY OF THE SAND WHITING (*SILLAGO CILIATA* C. & V.).*

By K. W. CLELAND.

(From the Department of Anatomy, University of Sydney.)

(Four Text-figures.)

[Read 28th May, 1947.]

I. INTRODUCTION.

The term "whiting" is a vernacular title and refers, in Australian waters, to the teleostean family Sillaginidae. The sand whiting of New South Wales and Queensland is the species *Sillago ciliata* (Cuvier and Valenciennes, 1829).

The Australian whitings comprise some four species of economic importance and are distributed along the east and south coasts of the continent. The species involved are: the sand whiting (*Sillago ciliata* C. & V.), the bass whiting (*S. bassensis* C. & V.), the trumpeter whiting (*S. maculata* Q. & G.), and the spotted whiting (*Sillaginodes punctatus* (C. & V.) Gill).

With the exception of the South Australian spotted whiting fishery, the whiting fisheries are of only minor economic importance, as Table 2 indicates.

The present paper is a technological discussion of the sand whiting fishery, and while incomplete, it is felt that it provides the basis for a rational control of the fishery.

Several abbreviations have been employed:

L.C.F. denotes length from the tip of the snout to the caudal fork, a measurement accurately and easily made. All lengths, unless otherwise stated, are L.C.F.'s. For conversion of L.C.F. to total lengths Table 1 is appended.

S.E. denotes standard error.

S.D. denotes standard deviation.

C.V. denotes coefficient of variation.

Sample Mean is the mean of the means of individual samples.

Single Sample denotes the characteristics of a sample of fish collected at one point in space and time.

L1, 2, 3, etc., represent the intermediate lengths as calculated from the rings on the scales.

The work embodied in this paper was carried out during 1942–44.

TABLE 1.

Conversion of L.C.F. to Total Lengths.

Length to caudal fork	150	170	190	210	230	250	270	290
To find the total length, add x mm. to L.C.F.	10	11	12	14	15	16	18	19

Unless otherwise stated, all conclusions, figures and tables refer to both Queensland and New South Wales populations.

R

Whiting Catches in the Various States.

	S. Aust.*	Qld.†	N.S.W.‡	Vict.**
Weight, lb./year	2,100,000	448,000	438,000	160,000
Per cent. total onshore fish	60	9·6	2·7	6·5
Per cent. Australian whiting	67	14	14	5
Approx. annual value	£150,000	£25,000	£25,000	£9,000
Main species	S. punct.	S. cil.	S. cil.	S. bass.
Period	1936–42	1936–42	1938–42	1911–41

C.V. of catch statistics, between years, is about 15%.
* South Australia, Department of Fisheries and Game, Reports, 1936–44.
†Queensland Fish Board, Annual Reports, 1 et seq.
‡ Manuscript Reports by the New South Wales Fisheries Department field inspectors, 1938–1944.
** Manuscript records of fish arriving at Melbourne Markets, 1911–1944.

II. TAXONOMY.

Genus SILLAGO Cuvier.

Sillago Cuvier 1817, *Reg. Anim.*, 2, p. 258; Swainson 1839, *Nat. Hist. Anim.*, 2, p. 205; Gill 1861, *Proc. Acad. Nat. Sci. Philad.*, p. 504; Boulenger 1910, *Ann. Nat. Hist.*, 8, p. 269.

SILLAGO CILIATA Cuvier and Valenciennes.

Cuvier and Valenciennes 1829, *Nat. Hist. Poiss.*, 3, p. 415; Gunther 1860, *Cat. Fish. Brit. Mus.*, 2, p. 245; Gill 1861, *Proc. Acad. Nat. Sci. Philad.*, p. 504; Jonan 1861, *Soc. Cherbourg. Mem.*, 8, p. 272; Steindachner 1866, *Sitz. Acad. Wiss. Wien.*, 53, p. 443; Kner 1869, *Reise. Novara. Fische*, p. 127; Castlenau 1873, *Proc. Zool. Soc. Vict.*, 2, p. 113; 1875, *Off. Rec. Philad. Cent. Exhib.*, p. 16; 1876, *Res. Fish Aust.*, p. 16; Alleyne and Macleay 1877, PROC. LINN. SOC. N.S.W., 1, p. 279; Klunzinger 1879, *Sitz. Acad. Wiss. Wien.*, 80, p. 369; Schmelz 1879, *Cat. Mus. Godeffroy*, 7, p. 44; Gunther 1880, *Chall. Exp. Rcps.*, 1, p. 42; Macleay 1881, PROC. LINN. Soc. N.S.W., 5, p. 567; 1881, *Desc. Cat. Aust. Fish.*, 1, p. 42; Woods 1882, *Fish. N.S.W.*, p. 65; Pohl 1884, *Cat. Mus. Godeffroy*, 9, p. 32; Ogilby 1886, *Cat. Fish. N.S.W.*, p. 31; Kent 1889, *Food Fish. Qld.*, p. 11; McCoy 1889, *Prod. Zool. Vict.*, 2, p. 299; Cohen 1892, *Mar. Fish and Fisheries, N.S.W.*, p. 16; Kent 1893, *Gt. Barrier Reef*, p. 293; Ogilby 1893, *Fish. N.S.W.*, p. 63; Waite 1901, *Rec. Aust. Mus.*, 4, p. 47; 1904, *Mem. N.S.W. Nat. Club*, 2, p. 31; Jordan and Seale 1905, *Bull. U.S. Bur. Fish.*, 25, p. 277; Stead 1906, *Fish Aust.*, p. 109; 1908, *Fish. N.S.W.*, p. 35; McCulloch 1911, *Endeavour Zool. Res.*, 1, p. 62; Roughley 1916, *Fish Aust.*, p. 90; Ogilby 1920, *Comm. Fish. Fisher. Qld.*; McCulloch 1927, *Fish. N.S.W.*, p. 50; Fowler 1928, *Mem. Bishop Mus.*, 10, p. 235; Weber and De Beaufort 1931, *Fish. Indo-Aust. Archip.*, 6, p. 178; Fowler 1933, *Bull. U.S. Nat. Mus.*, 100 (12), p. 428. SILLAGO CILIATA DIADOI: Whitley 1932, *Rec. Aust. Mus.*, 18, p. 344. SILLAGO BASSENSIS: Castlenau 1879, PROC. LINN. Soc. N.S.W., 3, p. 381; Macleay 1881, *Ibid.*, 5, p. 567; Kent 1893, *Gt. Barrier Reef*, p. 291; Tosh 1903, *Proc. Roy. Soc. Qld.*, 17, p. 175. SILLAGO DIADOI: Tholliere 1856, *Ann. Soc. Imp. Agric. Hist. Nat. Lyons*, 8, p. 351; Tholliere 1857, *Fauna Woodlark*, p. 151. SILLAGO GRACILIS: Whitley 1932, *Gt. Barrier Reef Exp.* 4, No. 9. SILLAGO INSULARIS: Castlenau 1873, *Proc. Zool. Soc. Vict.*, 2, p. 113. SILLAGO TERRAE-REGINAE: Castlenau 1873, PROC. LINN. Soc. N.S.W., 2, p. 232.

No attempt will be made here to give a full taxonomic description of the fish, but, for rapid identification in the field, the following simple key has been constructed.

1. Spot at base of pectoral fin.
   .1 Slight longitudinal lateral band .... *ciliata* (C. & V.)
   .2 Pronounced band .... *maculata* (Q. & G.)
2. No spot at base of pectoral fin.
   .1 Body with rusty red blotches .... *bassensis* (C. & V.)
   .2 Body without rusty red blotches.
      .21 Anal fin with 20 spines and rays .... *robusta* (Stead)
      .22 Anal fin with 24 spines and rays .... *sihama* (Forskal)

These are the only whitings likely to be found on the east coast of Australia.

III. THE FISHERY.

1. General.

The sand whiting is a typical onshore fish occurring in the estuaries, bays, lakes and surf of the east coast of Australia. The normal habitat appears to be the sand flats, and to a lesser extent the mud flats, in water of up to three fathoms deep. Using the catch statistics of New South Wales, and expressing the whiting catch as a percentage of the total fish (less the travelling mullet) caught at the various stations,

no difference could be demonstrated in the productivity of bays and lakes as compared
with estuaries. The fish appears to congregate about the mouths of estuaries, but
may be found for a considerable distance upstream.

2. Distribution.

The distribution of fish along the coast of New South Wales was analysed by
dividing the coast into ten areas, corresponding to the latitude parallels; these data
are summarized in Table 3. Row A shows the percentage which the whiting taken
in the area is of the State total whiting landings; row B shows the percentage which
the whiting landing makes of the total fish, less travelling mullet, landed in the area,
and thus the proportion which the whiting makes of the fish indigenous to the area.

TABLE 3.
Distribution of Sand Whiting along the Coast of New South Wales.

Area		1	2	3	4	5	6	7	8	9	10
A		7·5%	7·6%	11·3%	9·3%	21·9%	21·9%	8·3%	8·3%	2·5%	0·2%
B		7·5%	7·4%	4·8%	8·0%	10·1%	5·6%	5·3%	2·4%	1·4%	0·13%
Latitude		28–9	29–30	30–1	31–2	32–3	33–4	34–5	35–6	36–7	37–8
Main stn.		Richmond River	Clarence River	Coff's Harbour	Port Macquarie	Port Stephens	Lake Macquarie	Lake Illawarra	Jervis Bay		

After this paper was written, statistics became available showing that three-
quarters of the Queensland whiting catch comes from the three stations Gympie,
Maryborough and Wynnum.

3. Fishing Methods.

A. *Methods using Mesh Nets.*

(i). *Working from Mud or Sand Flat.*—One fisherman holding one end of the net
is landed on the flat, or in shallow water near the flat, while the other rows in an
approximate circle and casts the net. The first man, carrying his end of the net with
him, rejoins the boat. One of the ends is fixed to a rowlock and the net drawn in
from the other end. One of the men beats the bottom with an oar to scare the fish,
and thus cause them to enmesh themselves.

(ii).·*Working with Sea Anchor.*—One end of the net is fastened to a basket which
acts as an anchor. The method, in effect, dispenses with the first fisherman in method
(i), but is otherwise the same. It is used in deeper water.

(iii). *Using Tide in Shallow Water.*—At high tide a stake is driven into the flat,
and one end of the net tied to it; the net is then cast and the other end tied to the
same stake. The net may be supported by stakes driven in along its circumference.
Apparently wire netting is sometimes used in place of the net. When the tide goes
down, the fish are collected from the meshes of the net or from the flat itself.

(iv). *Using Two Boats.*—In order to reduce the loss of fish due to disturbance of
the water while casting, the net may be loaded equally on two boats, both of which
cast. This reduces the casting time by half, and causes less disturbance of the water.
Otherwise the method is similar to (i).

B. *Methods using Hauling Nets.*

Because they are necessarily of larger mesh, hauling nets are not really adapted
for the capture of a fish of this shape; however, a considerable part of the landings is
said to be made by this method. Kesteven (1942) has given a full account of the
hauling nets and their methods of use.

The mesh nets of New South Wales must, by law, be not smaller than 2¼" in mesh,
except in the Clarence River, where mesh nets of 2½" are allowed, and in Port Stephens,
where nets must not be smaller than 1½" in mesh. The nets may be up to 50 fathoms
long.

The boats used are the usual on-shore fishing boat, about 18 feet long. The value
of the net is £10–20, and the boat about £50.

4. *Seasons of Fishing.*

The monthly landings in New South Wales show a maximum in summer and a minimum in winter, while in Queensland the maximum catches are made in late winter and early spring, as Table 4 indicates. The figures were arrived at by assuming an equal monthly catch and expressing the actual catch in each month as a percentage of this theoretical catch, thus making 100% equivalent to approximately 37,000 lb. of fish. The coefficient of variation of these data is approximately 15%. The cycle is thought to be due to increased gregariousness during the reproductive season.

TABLE 4.

Monthly Landings of Sand Whiting in New South Wales and Queensland.

			Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
N.S.W.	..	..	126	113	114	100	90	88	88	78	66	97	120	104
Qld.	..	..	70	76	80	75	88	106	117	135	137	110	96	94

5. *Marketing.*

Marketing arrangements appear to be satisfactory, less than 0·5% of all fish being condemned in Sydney markets, and whiting does not make a disproportionate part of these.

6. *Existing Control.*

Methods used in the control of the fishery are:

(i). Fixation of the minimum legal length at 9½″ in New South Wales and 9″ in Queensland.

(ii). Fixation of net mesh as described above.

(iii). General method of closing certain waters to all or certain types of fishing.

IV. BIOLOGY.

1. *Raciation.*

As far as can be seen at present there is no conclusive evidence of raciation in these stocks. Whitley (1932) has granted to the Queensland specimens the rank of subspecies, but there appears to be no evidence to support this split, nor does Whitley appear to give any valid reason for making it.

The following characters were investigated on small samples of fish from each State.

A. *Morphological.*

(i). *Fin Ray Counts.*—No significant difference was found in the counts of the two diagnostic fins—the soft dorsal and the anal. The range was 17–19 rays and spines.

(ii). *Vertebrae.*—Twenty skeletons only were investigated. No difference was detected in these small numbers, counts of 33–34 being obtained. However, the numbers are too small to permit of a dogmatic statement.

(iii). *Scales.*—The scale count was made along the lateral line to the base of the caudal peduncle. The range 62–70 was found, but there was no significant difference between the two series.

It is doubtful if a difference in these characters could be called genetic as, according to recent work of Gabriel (1944), environment has a considerable effect.

(iv). *Body Proportions.*—Ten measurements were made on each fish, including length, breadth and height, but no significant differences were detected in the regression coefficients or the characteristics of Huxley's heterauxesis equation.

B. *Physiological.*

(i). *Spawning Time.*—There is a difference of three months in the spawning times of the Queensland and New South Wales fish. Whether or not this may be interpreted as evidence of physiological raciation depends on the physiology of the induction of spawning in this fish.

The induction of maturation and spawning in animals is thought to be governed by two main factors:

(1). Temperature, both as critical temperature and temperature change, which appears to be the factor in invertebrates and in some of the lower vertebrates. See Bullough (1939) and Moore (1942) for literature.

(2). Photoperiodism is the governing factor in most mammals, and it has been shown to be a factor in some fish. See Bullough (1939) and Marshall (1942) for literature.

The question now arises: can the difference of three months in the spawning time of the Queensland and New South Wales fish be shown to be due to either of these factors?

With regard to temperature, an inspection of the available surface isotherms of the two main fishing centres shows that a difference of 5° exists. This may or may not be sufficient to account for the observed difference in spawning time. If, indeed, temperature is the governing factor, the difference, by analogy with other cases investigated, may be sufficient.

When one plots the values for mean civil daylight for latitudes S. 25 and 32½ (Nautical Almanac) and compares the graphs planimetrically, the periods (a) from the end of spawning to the beginning of discernible maturation and (b) from the beginning of maturation to the spawning act show considerable differences in total daylight hours in the two States. Indeed similar calendar periods agree more closely than the biological periods delimited above, as Table 5 shows. The figures refer to planimetric figures only.

TABLE 5.

Period				Feb.-Aug.	Nov.-May.	Aug.-Jan.	Apr.-Sept.
N.S.W.	..	..		(a) 3,430	3,981	(b) 3,931	3,052
Qld.	..	..	..	3,527	(a) 3,905	3,802	(b) 3,376

A further complication was indicated by Bullough's (1939) work on the minnow. He showed that there was a critical temperature for the operation of the photoperiodic response, and this may explain the above unexpected results.

(ii). *Growth Rates.*—As Table 6 indicates, no significant difference between the growth rates of samples from the two States was found. The apparent significant difference in L2 is explained later.

TABLE 6.
Growth Rates in New South Wales and Queensland Samples.

				L1.	S.E.	L2.	S.E.	L3.	S.E.
Qld.	..	..	..	156	2·3	247	1·7	284·7	4·0
N.S.W.	..	..	..	150	3·1	241·6	1·3	285·7	2·7

It is difficult to give a satisfactory explanation of this equivalence. Knowledge of the effect of temperature on the growth of animals is still in an unsatisfactory state, but the records available indicate considerable complexity of the response.

The general finding that higher temperatures give smaller adults is not borne out here, neither does the acceleration of growth rate *per se* appear. See Belehradek (1936) and Fox (1939) for literature.

Two hypotheses are capable of explaining these data: (a) That the Fox effect is operating here, and that adaptation to higher temperatures has occurred. This would be no argument against homogeneity of stocks. (b) That there is a genetic adaptation to higher temperatures and that the similarity is an indication of some degree of raciation of the stocks.

(iii). *Ponderal Index.*—A difference approaching significance was found in the two sets of data, but the Queensland samples consisted of only 100 fish. The values of $k(\times 10^6)$ of the equation $W = kL^3$ were: Queensland 354 (S.E. 2·1), New South Wales 350 (S.E. 2·5).

While the possibility exists that raciation of a subtle kind may be present in the stocks, there is certainly no evidence for Whitley's subspeciation. For the purposes of the economic biology of the fish it has been concluded that the populations of New South Wales and Queensland may be considered to be from the same stock.

2. *Food.*

The small number of stomach contents examined showed only annelids and crustaceans. This, however, is in accord with fishermen's reports and the records of the earlier investigators. Tosh (1903) records much the same dietary for the Queensland fish.

3. *Reproduction.*

(i). *Gonad Maturation.*—In New South Wales, the fish begins to mature eggs for the next year's spawning in August–September. Most fish examined in September have pigmented ovaries and enlarging testes. The testes provide the most accurate index of the onset of maturation—they change from black, thread-like, to elongated, greyish, triangular bodies.

An attempt was made to follow this maturation by an arbitrary scale of gonad stages, but it was discarded as not being sufficiently accurate in the author's hands.

(ii). *Breeding Season.*—Since only five running ripe fish were taken during the present investigation, it is difficult to give accurate limits to the breeding season from direct sources.

A consideration of all data, both direct and indirect, led to the conclusion that the middle of the breeding season for the New South Wales populations was in January, with a total range of four months.

It is possible that the fish has two main spawnings in the year. One is led to this conclusion by the frequent trimodality of the ova-diameter frequency diagram—the modes representing: (*a*) immature non-maturing stock ova, (*b*) eggs of the second spawning, and (*c*) eggs of the first spawning. Furthermore, in large samples of first-year fish, the length frequency diagram often shows two modes. If true, the second spawning would follow closely on the first.

In Queensland, however, the mid-spawning time falls in September, with about the same range as the New South Wales season.

(iii). *Length at Sexual Maturity.*—The two-year-old fish definitely mature eggs and spawn, but the sexual maturity of the one-year-old fish is difficult to assess. The enquiry resolves itself into two aspects, (*a*) whether any eggs are matured and (*b*) whether any eggs matured are spawned and fertile.

Three types of ovary have been found in this first-year group:

(i). Glassy ovaries which show no sign of maturing eggs.

(ii). Pigmented ovaries with a few histologically normal eggs.

(iii). Pigmented ovaries showing usual numbers of histologically normal eggs.

Conditions (i) and (ii) greatly predominate.

The question of whether such eggs as are present are effectively spawned is more difficult to answer: they may be reabsorbed in the ovary, they may be spawned and infertile, or they may be completely fertile. By analogy with other cases of neotenic sexuality and adolescent sterility, the fish have been classified as adolescent and their contribution to the reproductive potential of the stocks is considered negligible. Even if this group were completely fertile and all normally fecund, assuming a constant relation between gonad weight and body weight, twice the number would be required to give a reproductive potential equal to that of two-year fish. This is important in considering control measures.

The second-year group is certainly mature and this puts the length (L.C.F.) at first maturity at about 260 mm.

(iv). *Spawning Place.*—It seems likely that spawning takes place either in the mouths of the rivers, etc., or more probably, in the open sea. This opinion is based on the following evidence: (1). Reports from various sources, official and otherwise,

that in the breeding season large schools have been seen in the mouths of rivers making for the open sea. (ii). The occasional capture of whiting both by line and net on the ocean beaches in the neighbourhood of the natural habitat of the fish, and the visual identification of schools in the open sea. (iii). The infrequent appearance of ripe fish in the market catches. While this may be due to the very rapid terminal ripening of the eggs, it seems more likely to be due to the migration of the ripe fish from the fishing zone. (iv). The evidence brought forward in the previous section for the lack of clear-cut raciation implies some degree of genetic mixing, which could be accounted for by the larval and post-larval mixing which would occur with sea breeding.

(v). *Larval and Post-Larval Life.*—Tosh (1903) has described the egg, larva and embryo of this fish. The eggs are pelagic, and larval development takes one day at 26°C. After seven days at 22–23°C. the development of the gut is completed. According to the reports of New South Wales fishermen, schools of young whiting are seen along the shoreline in February and March. The post-larvae then migrate into deeper water and by June are no longer to be seen around the shoreline. Assuming that the eggs are subjected to the action of the Notonectian current, the times for development recorded by Tosh are adequate to give larval mixing over most of the coastline.

(vi). *Sex Ratio.*—The sex ratio differs significantly from the expected 50:50 ratio, being found to be 47·5 males to 52·5 females.

4. *Migrations.*

Fishermen seem to be in favour of the hypothesis that the fish migrate, but although the catch statistics at first seemed likely to give some information, no objective evidence on this problem was found.

5. *Ponderal Index.*

The relation between length and weight is adequately expressed by the equation $W = kL^3$. Weights were recorded in ounces and lengths in centimetres because of limitation of apparatus.

The characteristics of $k (\times 10^6)$ are indicated in Table 7. Dannevig (1903) has recorded data which agree fairly well with the present findings.

TABLE 7.
The Characteristics of $k(\times 10^6)$.

				Mean.	S.D.	S.E.	C.V.
Single sample	..	..	..	—	20	3·0	6%
Sample mean	..	..	..	350	6·8	2·5	2%

6. *Age Determination and Rate of Growth.*

(1). *The Scale.*—Cockerell (1915) has briefly described the scale of the sand whiting, but the following short description is included to indicate the method of scale reading.

The scale is approximately rectangular, but has the anterior ctenoid edge curved. Six to eight radii extend fanwise from the nucleus to the posterior edge and are roughly equally spaced. For purposes of description the scale may be divided into four triangles—two right-angled dorsal and ventral triangles (hereafter called lateral), one median isosceles triangle with the posterior edge as its base, and one small anterior isosceles triangle containing the ctenoid patch.

The nucleus is just above the midpoint of the base of the anterior triangle and is delimited by one or more circular circuli, and surrounded by more or less concentric subcircles, until these are transected by the radii. For the purposes of scale reading, the centre of the inner circle is taken as the growth origin.

The circuli of the median triangle are closely packed and transected by the radii, while the circuli of the lateral triangles are much less densely packed, communicating with about one in three of the median circuli. Changes in direction of these lateral circuli are here considered to be homologous with the ring of cycloid scales. The change is generally obvious and begins near the base of the lateral triangle, where two

contiguous groups of circuli are seen to be at an angle to one another. As the apex of the lateral triangle is approached, the angle between the two groups is no longer visible. When the first circulus of the new direction group is followed round to the median triangle and the circuli of this region examined, one may find (a) no differentiation, (b) a bunching of the circuli of the region, as in the classical ring, or (c) granulation or branching of the circuli. In most cases some evidence of the change may be found in the corresponding area of the median triangle, and no difficulty was experienced in tracing the break around to the antero-posterior scale axis.

. Scales for age determination were collected from just behind the posterior extremity of the pectoral fin; this region was found to give scales with the greatest ring definition. The scale was projected by the apparatus described by Kesteven and Proctor (1942). The first circulus of the new direction group was followed round to the antero-posterior projection axis, and the intermediate lengths read by the methods described by these authors.

   (a). *Abnormalities.*—Abnormalities were fairly common, the following being found:

   (i). Granulation of the nucleus. This was noticed especially in fish of over 300 mm. in length. Generally one ungranulated scale in the sample from the fish was found (about a dozen scales from each fish were taken), but if none could be found the position of the nucleus was estimated.

   (ii). Absence of rings. This was a common abnormality. Usually only one was absent, and those present were in the usual positions and were recorded. Absence of all rings was a common feature of scales collected from positions other than the one recommended.

   (iii). Reduplication of rings. This was a rare abnormality. When present, the scale was discarded.

   (iv). Presence of ring in only one lateral triangle. A reading was nevertheless made since it was proved that the reading so obtained was compatible with readings of normal scales from the fish.

   (v). Atypical break morphology. Considerable difficulty was experienced in reading the scales of fish more than three years old, because the breaks became atypical. The method is suitable only for fish of less than four years

   (b). *Validity of Intermediate Lengths read from Scales.*—The validity of the scale method has been shown by a large number of authors, and it is probably reasonable to assume that the method is valid in every case. However, it is desirable to give verification in special cases, especially of tropical and sub-tropical fish. In this investigation the following methods were used:

A. *Establishing Precision.*

   (i). Reproducibility in individual fish. Successive scales from the selected area were read, and the calculated intermediate lengths were found to agree. The coefficient of variation was 2·85%.

   (ii). Reproducibility in single samples of fish. When a single sample of fish was examined the calculated intermediate lengths were found to agree within themselves and to be groupable on a normal frequency curve. The calculated intermediate length for one-year fish could sometimes be shown to follow a bimodal frequency distribution, a result of the twice a year spawning. The coefficient of variation declines from 13% in the first year to 6% in the second.

   (iii). Reproducibility between samples of fish. There is good agreement between mean calculated intermediate lengths of samples after the first year. The coefficient of variation declines from 6% in the first year to 2% in the second.

B. *Establishing Accuracy.*

   (i). Agreement with length-frequency data. The length-frequency diagrams of samples taken in the season when the ring is laid down correspond to the frequency curves of the calculated intermediate lengths. This is shown in the arithmetic seasonal growth curve (Fig. 2).

(ii). Agreement from year to year. Scales taken over a period of four years give substantially the same calculated intermediate lengths, and there appears to be no appreciable change of growth rate from year to year. For example, the growth of the fish spawned in 1940 and 1941, as calculated from the scales, was 161 and 158 mm., respectively. The pooled S.E. was 2·45 and the difference was not significant. The figures for these two years represent the greater part of the scale reading data.

(iii). Agreement with mathematical theory. The data obtained fall on a smooth curve, and when plotted semi-logarithmically, all points but the first and second fall on a straight line. The reason for the ectopy of the first two points will be discussed later.

(c). *Time of Ring Formation.*—The age in months was calculated by determining the month in which the rings were laid down. This was done by plotting the percentage of rings laid down in the various months. Considerable difficulty was experienced in diagnosing a newly laid down ring and consequently the middle part of the curve had to be interpolated rather subjectively. This led to the hypothesis that by October, 50% of the rings had been laid down. Nothing has since been found to invalidate this hypothesis.

Thus the age in months corresponding to the consecutive rings is 10, 22, 34, 46, etc. The ring on the scales from Queensland fish was found to be laid down three months before that of the New South Wales fish and the ages corresponding to the rings are thus the same for both States. The ring may be laid down to a response to improving food conditions or as a response to the beginning of sexual maturation; the latter hypothesis seems the more likely, as it would account for the conditions in both States.

(1). *Rate of Growth in Length.*—As determined by scale reading, this is shown in Figure 1 with both arithmetic and logarithmic plotting. Figure 2 shows the seasonality of growth. It was constructed by including all data of scale reading and mean lengths of samples, and so represents the mean growth of the fish month by month.

In the logarithmic graph the first and second points do not fall on the straight line. Point 1 is so because it represents growth over the biologically poorest months of the year. The length reached after a full year of growth, as read from the seasonal graph, is 220 mm., and assuming constant growth rate through the year, the length reached in ten months would be 183 mm. This point falls much more closely on the line. The
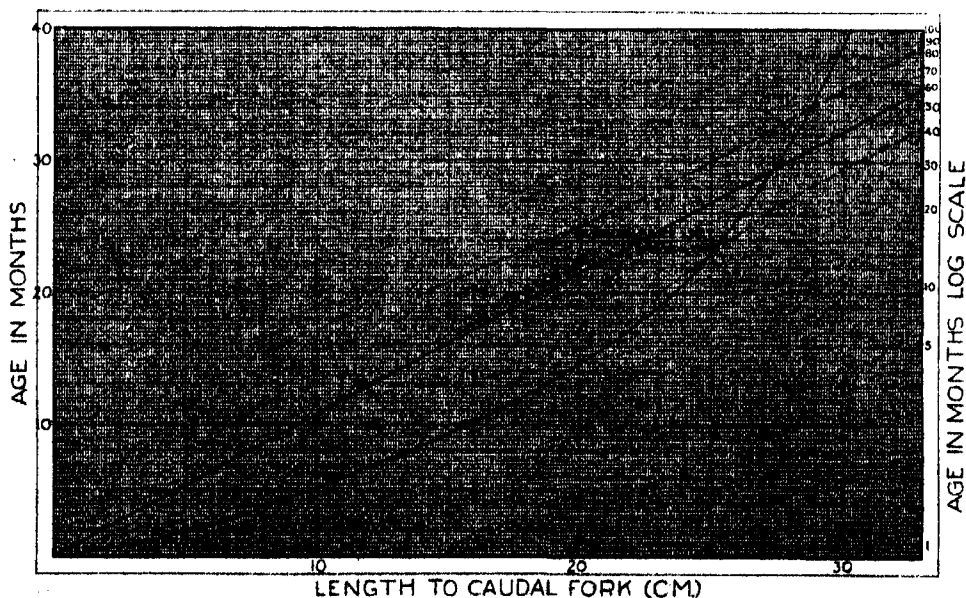
Fig. 1.—Rate of growth in length. Curve A shows arithmetic plotting and curve B shows logarithmic plotting. Scale data only.

second point is atypical because many of the New South Wales samples used for scale
reading were collected in the months when the rings were being laid down, and so only
the lower intermediate lengths are represented. This bias also appears in Figure 4. It
was also noted in the section on raciation.

The rate of growth in length is adequately expressed by the equation $Y = ab^x$, where
Y is the age in months, x is the L.C.F. in mm., and a and b are constants.
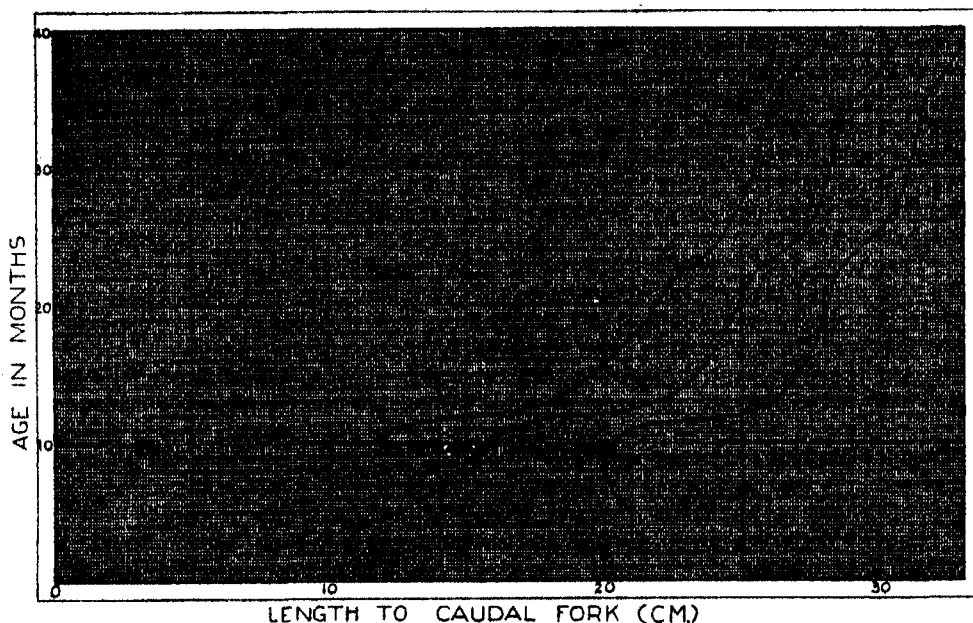
Fig. 2.—Showing the growth of the fish for each month of life. The curves were
constructed (a) from the scale data and (b) from the mean lengths of about 70 samples of
fish of one age group taken in various months of the year. Samples often contained only
one age group and no difficulty was experienced in separating age groups when more than
one was present.

No useful purpose would be served by recording all the scale data, but these data,
both for Queensland and New South Wales, are summarized adequately in Table 8.

TABLE 8.
Summary of Scale Data.

	L1.	S.D.	S.E.	C.V.	L2.	S.D.	S.E.	C.V.	L3.	S.D.	S.E.	C.V.	L4.	S.E.
Single sample ..	—	22	4	13%	—	14	4	6%	—	14	4·5	5%	—	3
Sample mean ..	158	10·5	3	6·7%	244	5	1·5	2%	285	6·8	3	2·5%	312	1·5

The largest New South Wales specimen obtained in the present investigation had
a length of 430 mm. and an estimated age of 18 years. The largest Queensland specimen
was 450 mm. long and its age was estimated as 22 years by the equation for rate
of growth in length.

(ii). *Rate of Growth in Weight.*—Figure 3 shows the rate of growth in weight.

The following equation fits the data: $X = K \dfrac{(\log. Y - \log. a)^2}{(\log. b)^2}$ where X is the weight in

ounces, Y the age in months, a and b are the constants in the length-growth equation,
and K the ponderal index. It will be seen that the growth is approximately arithmetic
for the first three years in life.
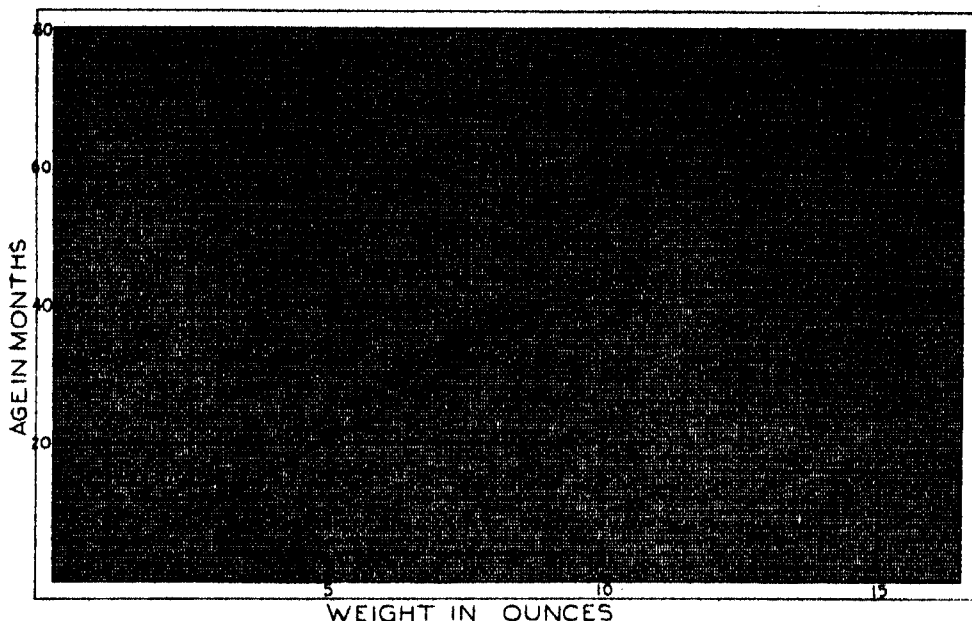
Fig. 3.—Rate of growth in weight.

7. *Pathology.*

The sand whiting has few parasites, either external or internal. Occasional worm parasites and neoplasms have been seen, but the only condition of economic importance is known to fishermen as "tarriness".

In this disease the fish is permeated by a peculiar tarry odour and taste which make it unfit for human consumption. The condition is apparently sporadic and not very common. Since no tarry whiting appeared during the time the author was in the markets no further description of the condition can be given.

V. CONDITION OF THE FISHERY.

1. *Economic Evidence.*

Catch statistics, except for two records in 1892 and 1893, which cannot be incorporated, exist for the period from 1938 onwards for New South Wales and from 1936 onwards for Queensland. It is impossible to trace trends over such a short period. Since most of the fisheries of Australia show some evidence of depletion (Kesteven, unpublished data), it seems likely that this fishery would also show economic evidence of this type also.

Fishermen are not inclined to express a definite opinion on this point, but there appears to be a suspicion that the fishing is not as good as it was. Fluctuations in a small fishery like this, especially long term ones, are not likely to impress fishermen until a state of serious depletion exists.

2. *Biological Evidence.*

New South Wales market measurements were available for a period of four years. Figure 4 is a frequency diagram of these data.

Queensland market measurements were available in small numbers for the period 1943–44. The numbers are only just on 3,000, but the sampling has been adequate. The frequency diagram is shown in Figure 4. In this figure the Queensland numbers have been multiplied by three to make the curves more directly comparable.

The minimum legal total lengths for both States and the desirable minimum legal length are also shown in Figure 4. The percentages of the fish below these various lengths are shown in Table 9.
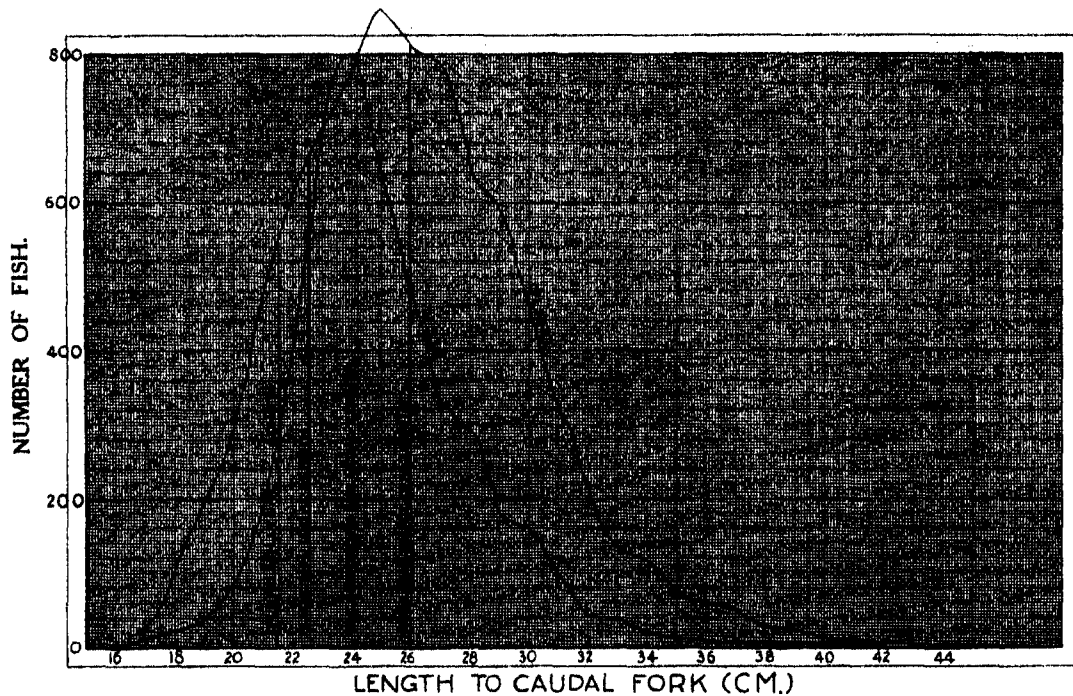
Fig. 4.—Frequency curves of the lengths of fish reaching Sydney and Brisbane markets. The Queensland figures have been multiplied by three to make the curves more readily comparable.

TABLE 9.

Percentages of Fish below Minimum Legal Length.

					N.S.W.	Qld.
Below Qld. minimum	..	..	..	9"	7·8%	13·0%
Below N.S.W. minimum	..	..	..	9½"	17·6%	20·9%
Below ideal minimum	..	..	..	10⅜"	68·6%	42·7%
Below recommended	..	..	..	10¼"	56·3%	52·9%

VI. SUGGESTIONS FOR CONTROL.

The following methods of control are suggested; their feasibility must be judged by those in administrative control of the fishery.

1. *Minimum Legal Length.*

It has been demonstrated that the existing minimum legal lengths are too low to protect the immature fish. A minimum legal total length of 275 mm. (10⅞") would be more in accord with biological fact, but an increase of 1¼" would almost certainly be tolerated by fishermen; for this reason a minimum legal length of 10¼" is recommended. This would not be subject to decrease even if conditions improve, and would, of course, apply in both States. It is interesting to note that Dannevig (1903) suggested 10¼" as the minimum marketable size of this fish.

2. *Regulation of Net Mesh.*

No further change in the existing New South Wales regulations would be required except to make them apply to the whole State. Netting experiments have shown that the 2¼" mesh is very destructive not only of immature whiting but also of other commercially important fish. It will enmesh fish at least as small as those shown in Table 10 and, of course, fish corresponding in shape to those recorded.

This control of net mesh would apply in both States and would not be liable to change if conditions improved.

TABLE 10.

Fish Enmeshed in Nets of 2¼″ Mesh.

Species.	L.C.F. (mm.).
Fantail mullet (*Mugil argenteus*)	200
Tano mullet (*Myxus elongatus*)	200
Sand whiting (*Sillago ciliata*)	180
Tarwhine (*Roughleia tarwhine*)	110
Silver Biddy (*Gerres ovatus*)	110
Herring (*Harengula castlenaui*)	120

The season when catches are greatest is also the time when the immature whiting becomes capable of capture by this net.

These suggestions for control would, if implemented, cause a fall in both numbers and weight of whiting caught, but in a year or two, while the numbers would be less, it is probable that the total weight landed would be considerably more than at present.

VII. SUMMARY.

(i). The landings of sand whiting in New South Wales and Queensland are approximately equal and are in the region of 500,000 lb. each per year and are valued at £25,000 in each State.

(ii). The taxonomic literature is listed and a simple key is appended.

(iii). In the area bounded by latitude S. 31 and latitude S. 34 the landings are greatest, but the fish is distributed along the entire coastline of New South Wales.

(iv). Mesh nets are most used for the capture of this fish, and the various ways of using them are listed.

(v). Maximum landings occur in summer in New South Wales and in early spring in Queensland.

(vi). There is no definite evidence of raciation in the stocks.

(vii). Food consists of the annelids and crustaceans of the mud and sand flats.

(viii). The breeding season for the New South Wales fish is from November to March and for the Queensland fish from July to November. Two spawnings may occur in this period.

(ix). The L.C.F. at first sexual maturity is 260 mm

(x). Spawning is thought to occur in the open sea.

(xi). The sex ratio is 47·5 males to 52·5 females.

(xii). No evidence of migration was found, but was thought to occur.

(xiii). The weight-length relation is expressed by the equation $W = 350L^3 \times 10^{-6}$, where W is the weight in oz. and L is the L.C.F. in mm.

(xiv). The scale and method of scale reading is described. A verification is made for the method.

(xv). Half the fish have breaks in the circuli by October.

(xvi). The rate of growth in length is expressed by the equation $L = 186 \log A$ where L is the L.C.F. in mm. and A is the age in months.

(xvii). The rate of growth in weight is expressed by the equation $W = 350 \dfrac{(\log A - 0 \cdot 028)^3}{146}$ where W is the weight in oz. and A the age in months.

(xviii). A large proportion of the market catches both in New South Wales and Queensland is made up of fish which have not yet spawned.

(xix). Recommended control methods are the raising of the minimum legal length to 10¼″ and the prohibition of mesh nets of less than 2½″ mesh, both provisions to hold in both States.

VIII. Acknowledgements.

IX. Bibliography.

Belehradek, J., 1936.—Temperature and Living Matter. Berlin.

Bullough, W. S., 1939.—A Study of the Reproductive Cycle of the Minnow in Relation to the Environment. *Proc. Zool. Soc. Lond.*, A, 109 : 79.

Cockerell, T. D. A., 1915.—The Scales of Some Australian Fishes. *Mem. Qld. Mus.*, 3 : 35.

Dannevig, H. C., 1903.—Notes on the Legal Weight of Food Fishes and their Lineal Equivalents. *Rep. Dept. Fish. N.S.W.*, 1903 : 60.

Fox, H. Munro, 1939.—The Activity and Metabolism of Poikilothermal Animals in Different Latitudes. v. *Proc. Zool. Soc. Lond.*, A, 109 : 141.

Gabriel, M. L., 1944.—Factors Affecting the Number and Form of Vertebrae in *Fundulus heteroclitus*. *J. Exp. Zool.*, 95 : 105.

Kesteven, G. L., 1942.—Studies in the Biology of Australian Mullet. i. Account of the Fishery and Preliminary Statement of the Biology of *Mugil dobula* Gunther. *Counc. Sci. Industr. Res.* (Aust.) Bull. No. 157.

————, and Proctor, Andrew, 1941.—A Modified Apparatus for Fish Scale Reading. *J. Counc. Sci. Industr. Res.* (Aust.), 14 (1) : 57.

Marshall, F. H. A., 1942.—Exteroceptive Factors in Sexual Periodicity. *Biol. Rev.*, 17 : 68.

Moore, J. A., 1942.—The Role of Temperature in the Speciation of Frogs. *Biol. Symposia*, 7 : 189.

Tosh, J. R., 1903.—On the Common Whiting of Moreton Bay (*Sillago bassensis*). *Proc. Roy. Soc. Qld.*, 17 : 175.

Whitley, G. P., 1932.—Studies in Ichthyology, No. 6. *Rec. Aust. Mus.*, 18 : 344.

MISCELLANEOUS NOTES ON AUSTRALIAN DIPTERA. XIII.*

THE ORIGIN OF THE VENA SPURIA.

By G. H. HARDY, Queensland University, Brisbane.

(Four Text-figures.)

[Read 30th July, 1947.]

The *vena spuria* is a thickened convex line of the wing membrane between the radial and median fields, a line seen in most Syrphidae. This takes a course in its usual length that reaches the apex of the median cell, and sometimes it is formed like the veins but is brown and translucent instead of black and opaque.

It is very evident that this is a *vena obsoleta* that may be still traceable as a complete vein in Diptera, and the only position that seems feasible for its occurrence in the primordial condition is in the highly reticulate venation such as that seen in some Nemestrinidae. The following observations are put forward in support of this view.

The search for the origin of the *vena spuria* started when Tillyard (1926) was about to publish his book on the *Insects of Australia and New Zealand*. However, in those days, the primitive radial sector was judged to be dichotomously twice branched, and this formed the basis of the search. When Alexander (1927) showed that a divergence of the vein direction may form a pectinate radial sector, a new search proved equally unsuccessful.

Recently, when attempting to homologize the veins within the Bombyliidae, the opinion was formed that the radial field became reduced there in a way that was not identical with the reduction presumed to have taken place in the Tabanoidea. It was thought that the latter reduction arose from developments seen to have taken place in the Nematocera, but in view of this new evidence, this must now be regarded as an erroneous conception.

Arising from observations on the venation of the Bombyliidae, it was deduced that here the radial field originally had five radial branches traceable and separated. A plan to include a primitive radial sector was worked out on the reticulate venation of *Nemestrinus osiris* Wied. The result was astonishingly close to a complete explanation for several characters in the Brachycera venation, characters which remained anomalous under the Comstock-Needham and the Tillyard notations.

Hypothetical Venation.—Figure 1 gives the reticulate venation, and certain veins are indicated by dots to suggest those that would form the pectinate four-branched radial sector. From the base of this radial sector arises another, but convex, branch which is responsible for that strongly convex diagonal vein that traverses the wing in the Nemestrinidae. The course of this extra vein V-S corresponds to the track along which the convex *vena spuria* is seen to lie in the Syrphidae, as also that of the crease similarly placed in various families of the lower Brachycera.

The interpretation given here is not satisfactory in all details. Obviously a concave vein section of the upper median branch is eliminated from the Nemestrinidae and retained in the other families mentioned. On this account at least the hypothetical archaic venation cannot be truly represented by the Nemestrinidae beyond about the basal half of the wing, where the *vena spuria* is being traced in this paper, the remainder being left for future solution.

The divergence from, and convergence towards, the vein Sc by the stem vein R is exhibited in Macquart's figure which is reproduced here. This is a feature seen in many wings of fossil Mecoptera and in those of primitive fossil orders, but it is very doubtful if the character can have been retained in any extant Diptera. None of Lichwardt's figures of venations of Nemestrinidae shows it, nor yet does Macquart show it other than in *Nemestrinus*.

The venation of the median field cannot be discussed until the primordial features are known, but in the figures given here it is shown that the veins M_x and M_4 of taxonomy represent highly complex veins in the Nemestrinidae and Mydaidae.

Nemestrinidae.—Figure 2 gives the same reticulation, retaining those veins which suggest that the venation of the genus *Trichophthalma* may evolve from it. The vein marked R_5 is the vein with the notation M_1 in taxonomy, and its original alliance with the radial field is obscure, as a cross-vein marked *c* connects it to the median field. The letter *b* marks the position of another cross-vein found between fields in Diptera, and *a* is the normal radial-median cross-vein of taxonomy.

Cyrtidae.—In Part xii of this series, the venation of *Panops* was given in Figure 1 with the convexity and concavity of veins indicated. If, on that figure, a vertical line be drawn adjacent to the first furcation of the median vein, this line will cross eight veins, marked in Figure 1 as being C, Sc, R_1, R_x, V-S, M, Cu and A. These veins are alternately convex and concave on *Panops*, making R_x concave and V-S convex.

As this is found to be consistent in Diptera, then, in theory, where these two veins come together, the convex vein marks the retention of V-S, the concave vein being R_x. It is usual to find that R_x branches from R_1 and proceeds in continuity with a strong convex vein wherever there is no other sign of a *vena spuria*.

Mydaidae.—In the genus *Diochlistus* the radial veins do not follow quite the same route as those in *Trichophthalma*, and Figure 3 is based upon the same reticulation to show this. Apically, the four uppermost radial branches are joined by cross-veins and three of the branch veins do not reach the wing margin; this gives the appearance of four veins converging to a point. In addition, there is a stump-vein on R_3.

Asilidae.—The genus *Phellus* and some other genera have R_x and V-S adjacent to each other, lying almost contiguously. However, V-S is reduced to a prominent ridge, along which flecks of brown membrane may be more or less retained, till it joins R_x to continue in a strongly convex vein. Here the basal part of V-S evidently disappears in advanced genera.

Syrphidae.—In this family the *vena spuria* lies well apart from the radial field and, when complete, it arises from that basal cross-vein between R and M. Basally it approaches R, but apically it slopes towards M, ending near the furcation of the uppermost median vein. It is questionable whether the branch vein R_5 is retained in this family.

Tanyderidae.—The genus *Radinoderus* has a recurrent stump-vein in the position of the vein V-S, and evidently this is a remnant left at the base of R_5. In Figure 4 the venation is traced from the same reticulation to show the probable homologies.

It would seem that an error was made in regarding the Tabanoidea as having arisen from the Nematocera with a venation like that of the Tanyderidae. These two arose independently from an ancestor with a common reticulate venation.

Remarks and Conclusions.—Theoretically, from the base of V-S to the apex of R_3 the vein is convex, but this is not always apparent throughout, owing to the flattening of the wing in its apical third. Being convex, this vein may be regarded as one unit standing apart from the radial field, and indeed, it may have become quite eliminated in the Cyclorrhapha, except for its traces left in the Syrphidae. If this be so, then the Cyclorrhapha may have only three radial branches, with R_3 and R_4 amalgamated to form the third.

In a letter dated 22nd January, 1947, Dr. C. P. Alexander informed me that Vignon and Séguy (1929) consider the *vena spuria* of the Syrphidae to be the vein MA (anterior median), and it must be noted that the radial sector in this family is reduced to two branches, one obviously compounded with two veins, making three branches detected.

This venational development is too far advanced to make certain of the relationship, but tracing the structure back to the Nemestrinidae with four branches in the radial sector does suggest that in the Syrphidae the *vena spuria* at least incorporates MA

On the other hand Tillyard (*Amer J Sci* ix 1925 p 331) remarks Thus it is actually not the posterior median which appears to be missing in recent insects but the anterior median or convex portion of the media this is not missing but has
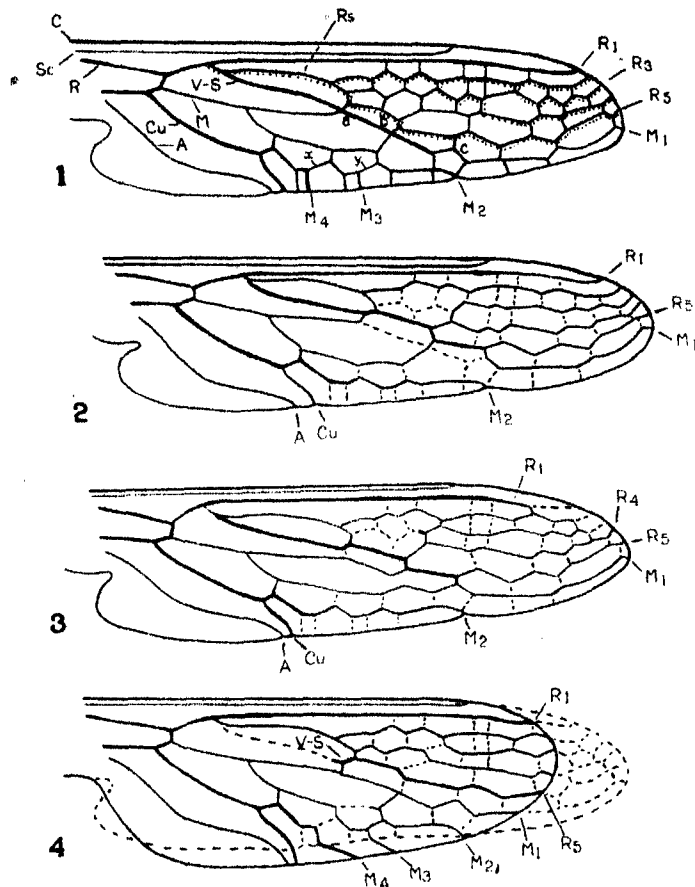
Fig. 1.—A reticulate venation found in *Nemestrinus*. The dots along the veins show those that form a four-branched pectinate radial sector. The convex vein V-S lies between the concave veins R_s and M, this being the position of the convex *vena spuria* in the Syrphidae.

To the Comstock and Needham notation of veins are added here the letters V-S, the homologue of the *vena spuria*: a, b and c, the three radial median cross-veins detected in the Syrphidae; x and y, the two cross-veins sometimes found in the median field.

The dots along the veins denote four branches of the pectinate radial sector which can be developed from this complex venation.

Fig. 2.—The same reticulation retaining the veins corresponding to those of the genus *Trichophthalma*. The vein R_5 is that which bears the notation M_1 in taxonomy.

Fig. 3.—The same reticulation retaining veins corresponding to those of the genus *Diochlistus*. The vein R_1 lies in continuity with cross-veins near the apices of incomplete R_2 and R_3 and complete R_4. This shows a reduction in length of the three upper longitudinal branches, which, in appearance, converge towards the fourth, ending in a common point. R_3 retains a stump-vein.

Fig. 4.—The same reticulation retaining veins corresponding to those of *Rhadinoderus*. The vein V-S is reduced to a stump, and a cross-vein is inserted between Sc and R_1. The radial sector is dichotomously twice branched in this genus of the Nematocera, a feature that has not been noted in any Brachycera. However, R_5 is always a convex vein and may not belong strictly to the radial sector.

become attached permanently to R, forming that portion of it which Comstock calls R₄₊₅." Later, Tillyard (Ibid., xi, 1926, p. 135) changed his opinion, stating: "MA, attached to MP in Paleodictyoptera, is attached to R. in Plectoptera and Odonata, but appears to be entirely missing in most recent orders", and he further specifies its absence in fossil and recent Mecoptera, concluding that it is eliminated throughout the Panorpoid Complex. Had Tillyard seen a fossil wing of a dipteron with the reticulated venation, doubtless he would have placed it in the Plectoptera, on evidence of venation, or else would have proposed a new order for its reception. Tillyard's later view seems to be erroneous.

Conclusions to be drawn at present suggest that:

(a). The *vena spuria* in the Syrphidae is a *vena obsoleta*, preserved as a main vein in various families of the Tabanoidea and Asiloidea, but its basal part is lost in the Nematocera.

(b). The Brachycera did not evolve its venation from any wing type seen in the Nematocera, but had a separate development from a reticulate venation. Also the Brachycera retains more of the archaic venation than does the Nematocera.

(c). Veins do not move from their original course to the extent usually assumed, but instead, different veins survive in the network of the reticulate venation, thus laying down more than one simplified venational foundation within the order.

(d). Convexity and concavity of veins are characters assuming greater importance than usually admitted in the study of Diptera. Presumably a convex and a concave vein should not be regarded as homologous in the absence of definite evidence that a change in character has taken place.

REFERENCES.

ALEXANDER, C. P., 1928.—Proc. LINN. Soc. N.S.W., 53 : 370, figs. 3 and 4 (*Rodinoderus*).
HARDY, G. H., 1925.—Ibid., 50 : 141, fig. 1 (*Diochlistus*).
————, 1945.—Ibid., 70 : 142, fig. 1 (*Trichophthalma*).
————, 1946.—Ibid., 71 : 67, fig. 1 (*Panops*).
MACQUART, P., 1840.—*Dipt. Exot.*, ii, Pl. 2, fig. 2 (*Nemestrinus*).

Fossil Leaves from Australian Brown Coal.

PLATE IX.
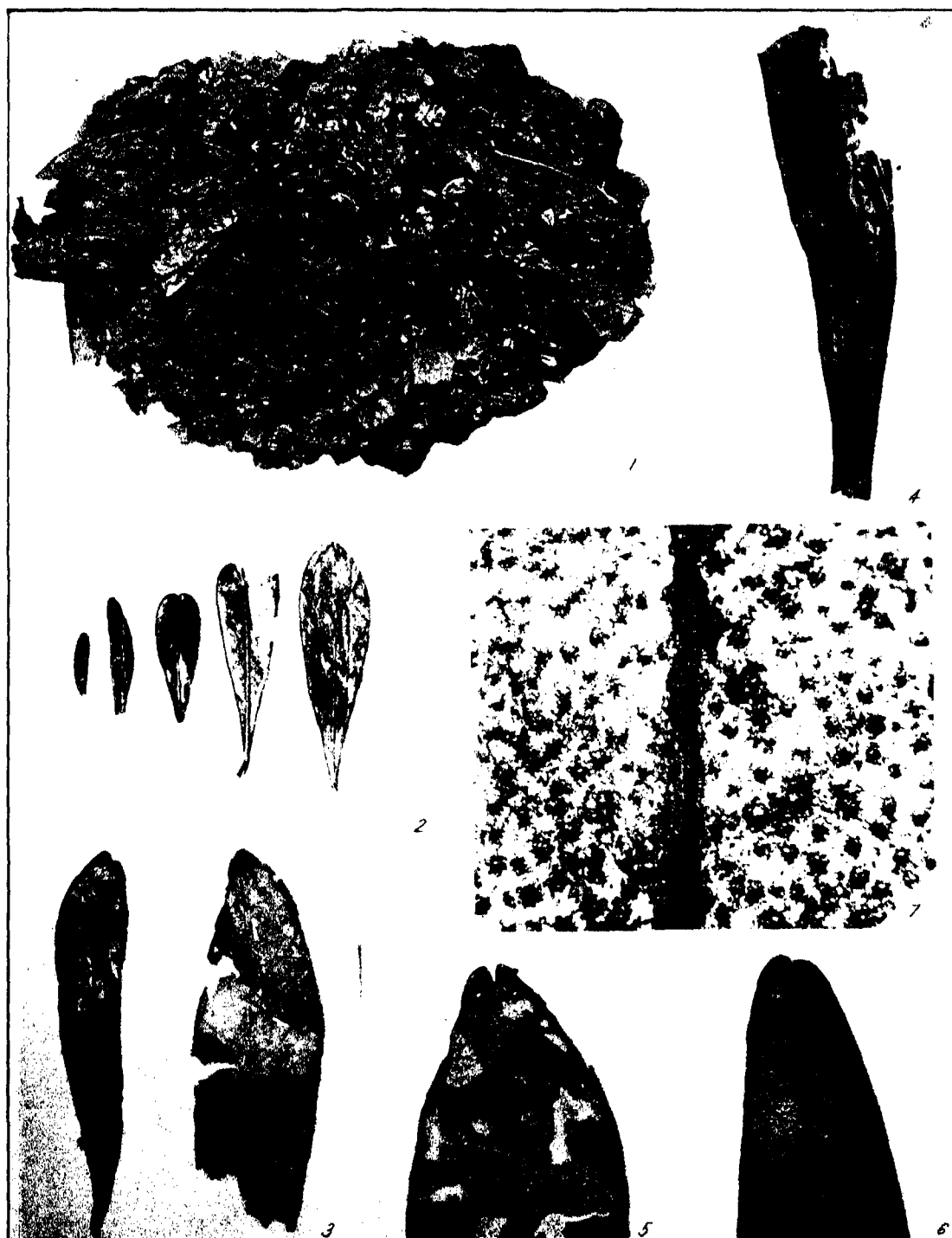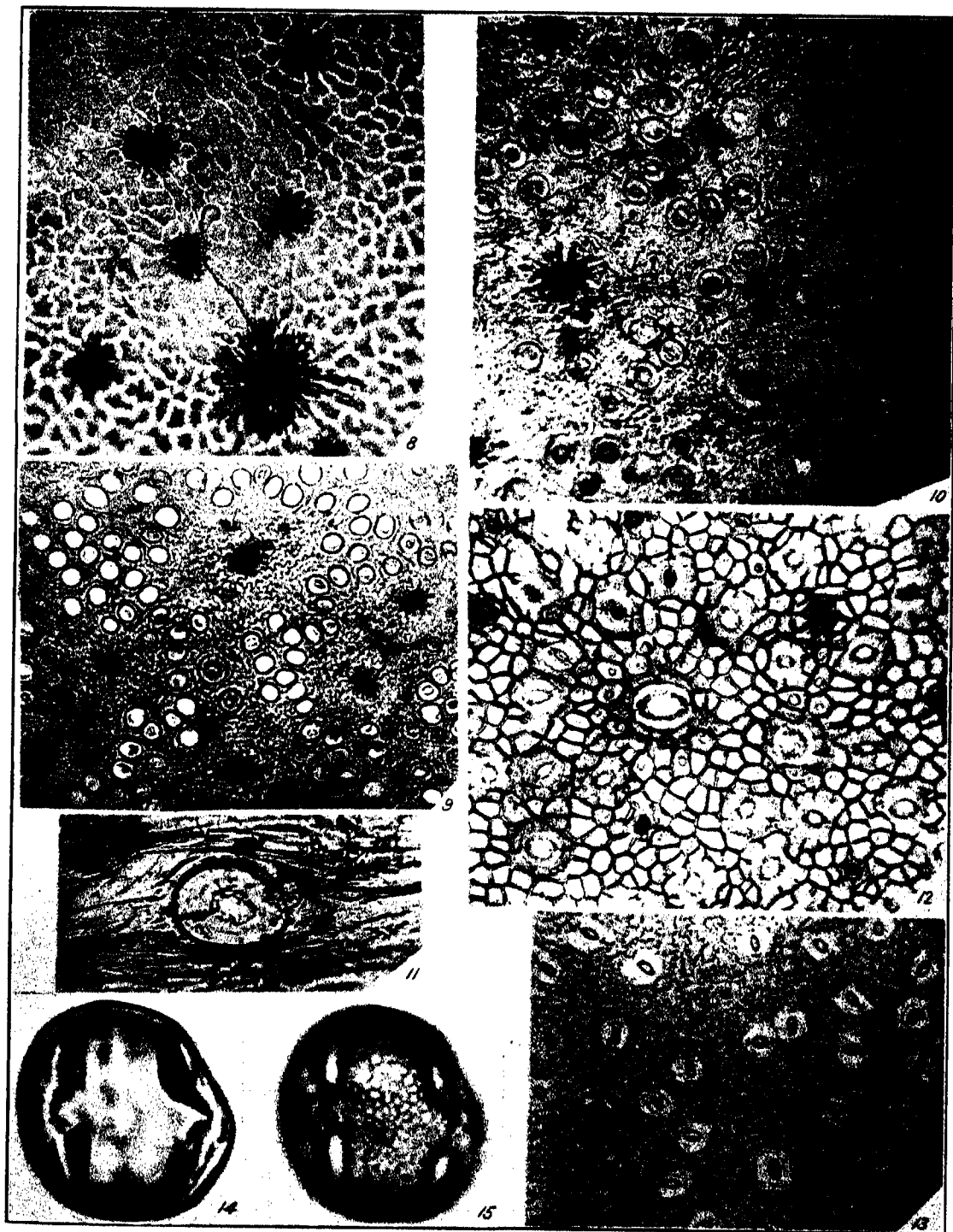
Fossil Leaves from Australian Brown Coal.

Fossil Leaves from Australian Brown Coal.
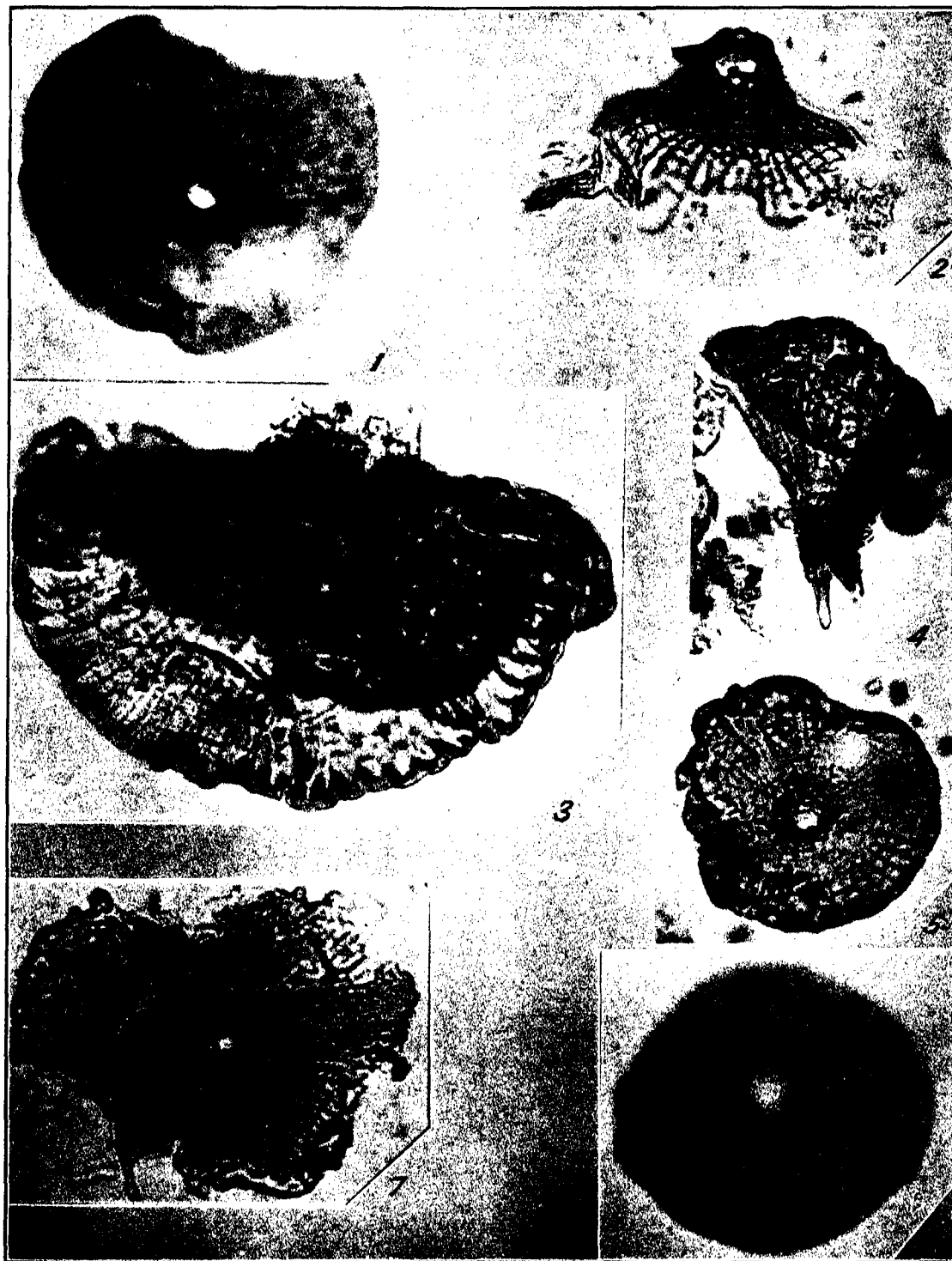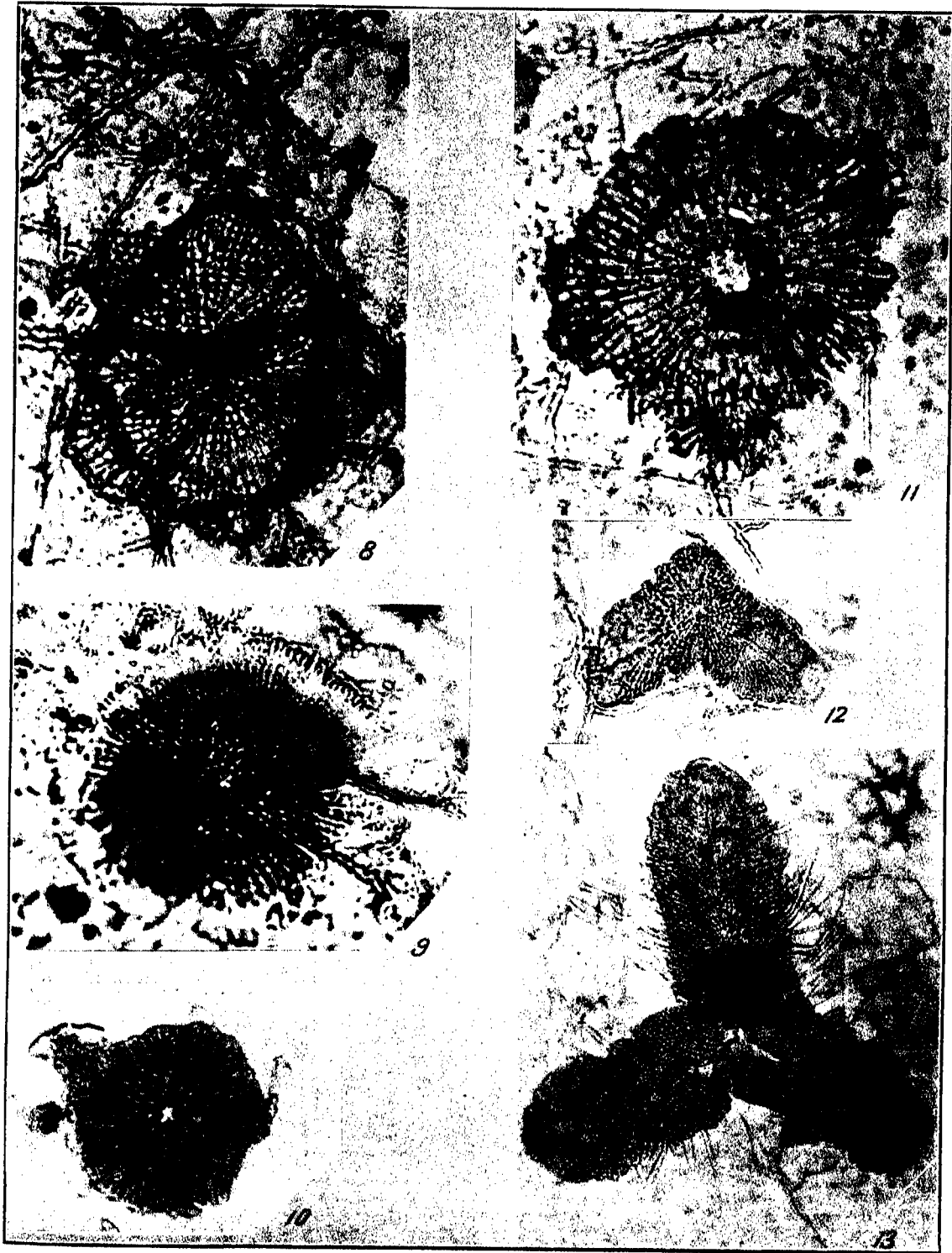
PLATE XI.

Fossil Fungi from Tertiary Deposits in the Southern Hemisphere.

PLATE XII.

Fossil Fungi from Tertiary Deposits in the Southern Hemisphere.

PLATE XIII.

Fossil Fungi from Tertiary Deposits in the Southern Hemisphere.

PLATE XIV.
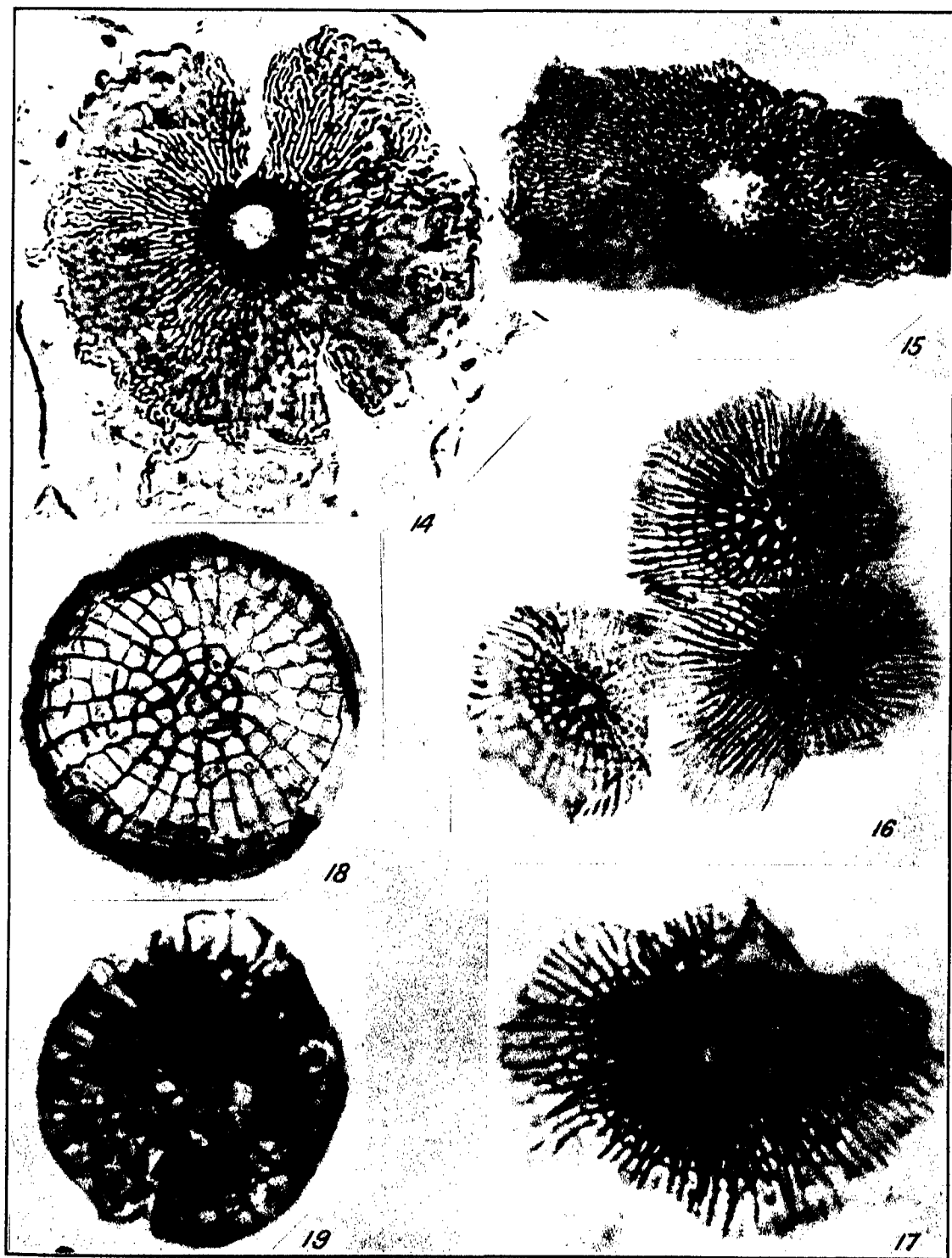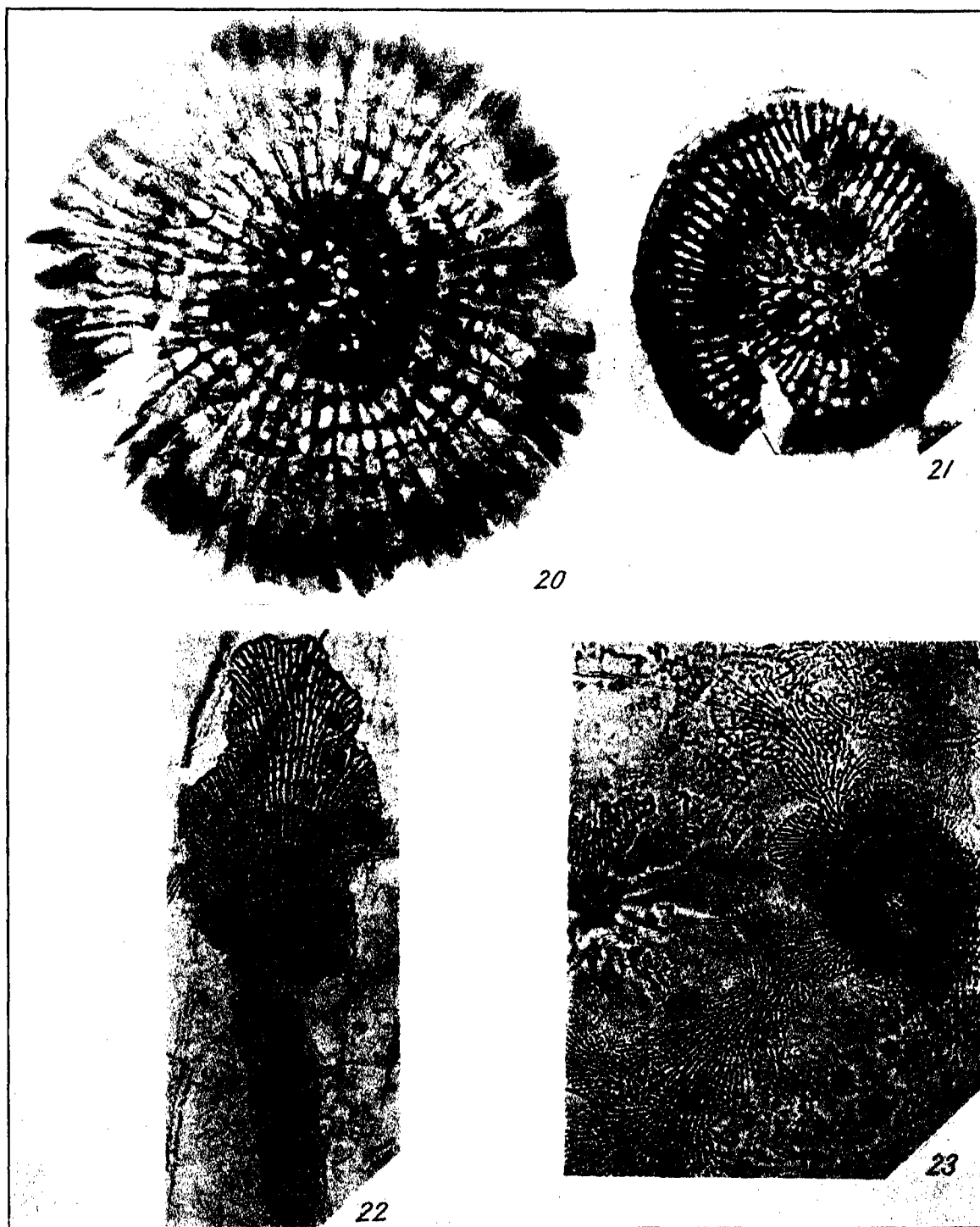
Fossil Fungi from Tertiary Deposits in the Southern Hemisphere.

Oogenesis in the Sydney Rock Oyster.
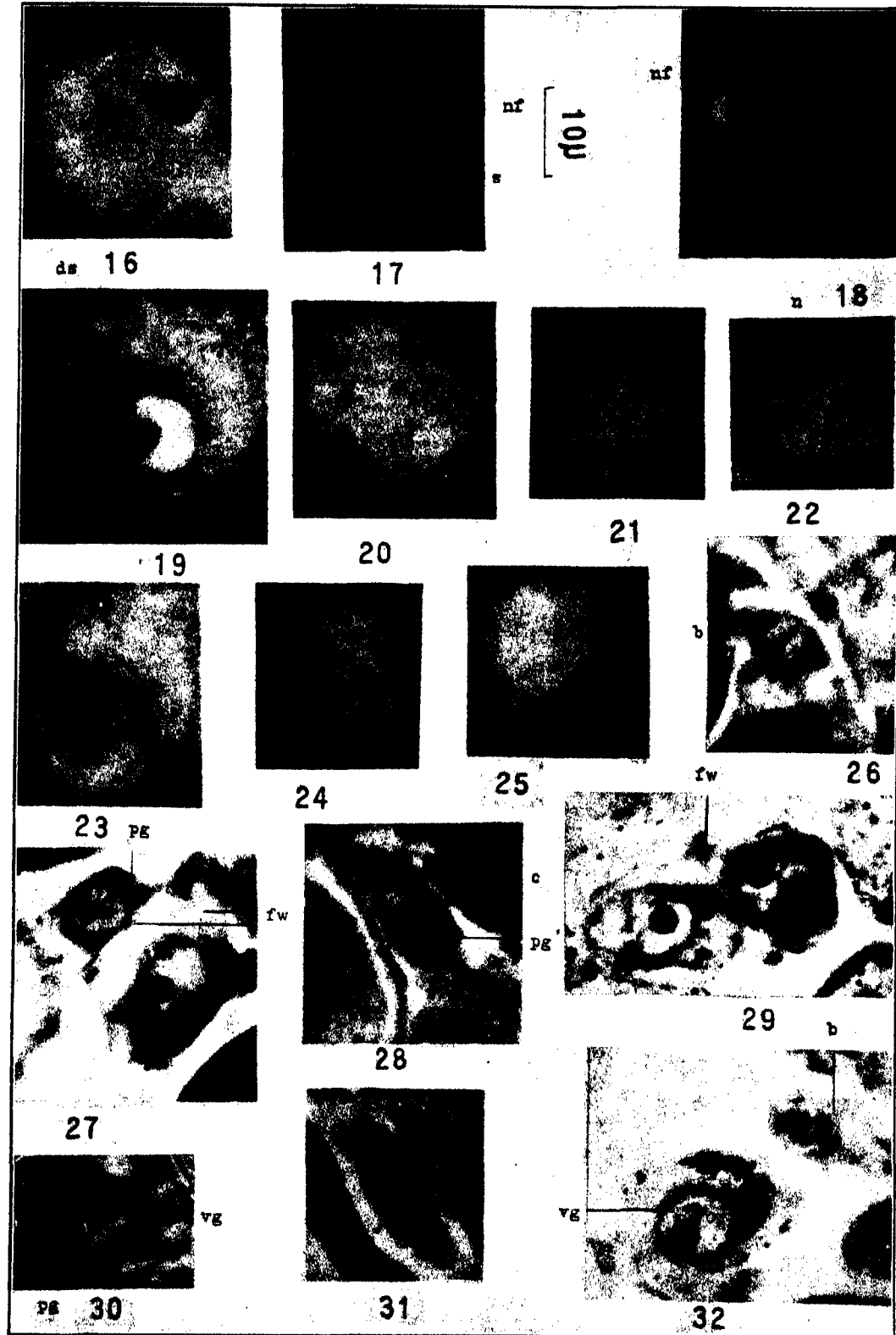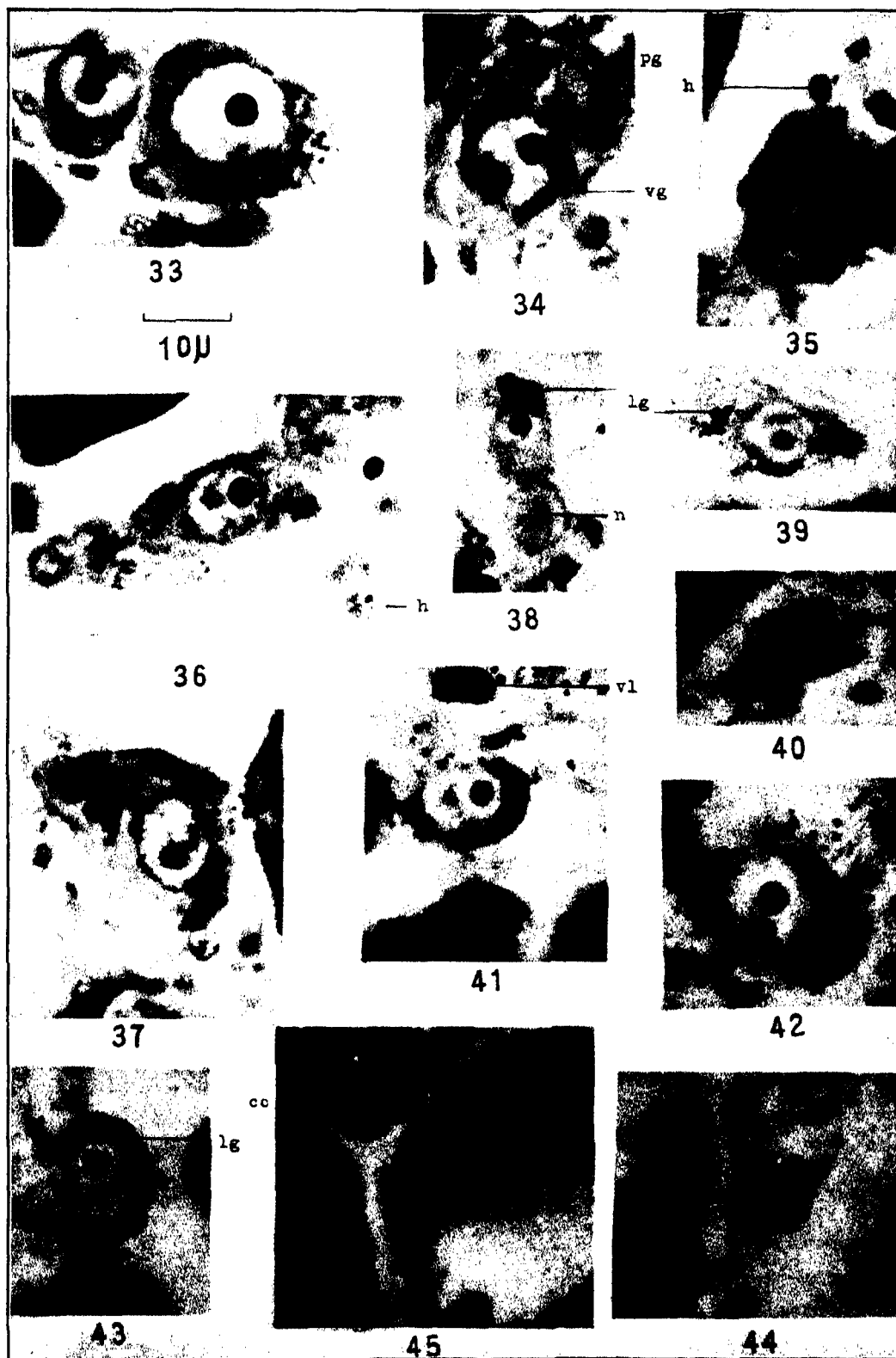
Oogenesis in the Sydney Rock Oyster.

Oogenesis in the Sydney Rock Oyster.

PLATE XIX.

Oogenesis in the Sydney Rock Oyster.

PLATE XX.

Oogenesis in the Sydney Rock Oyster.

.

PLATE XXI.
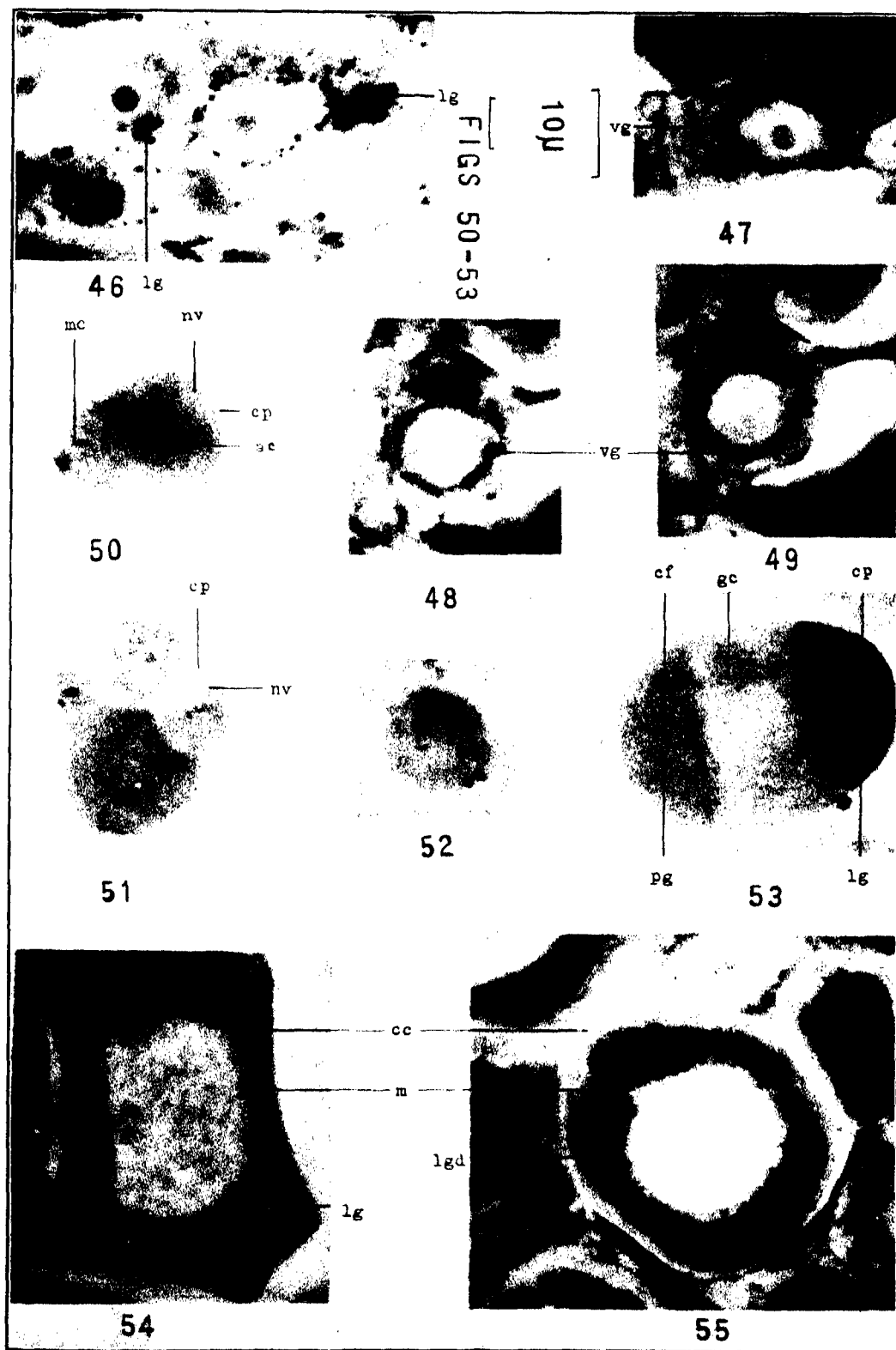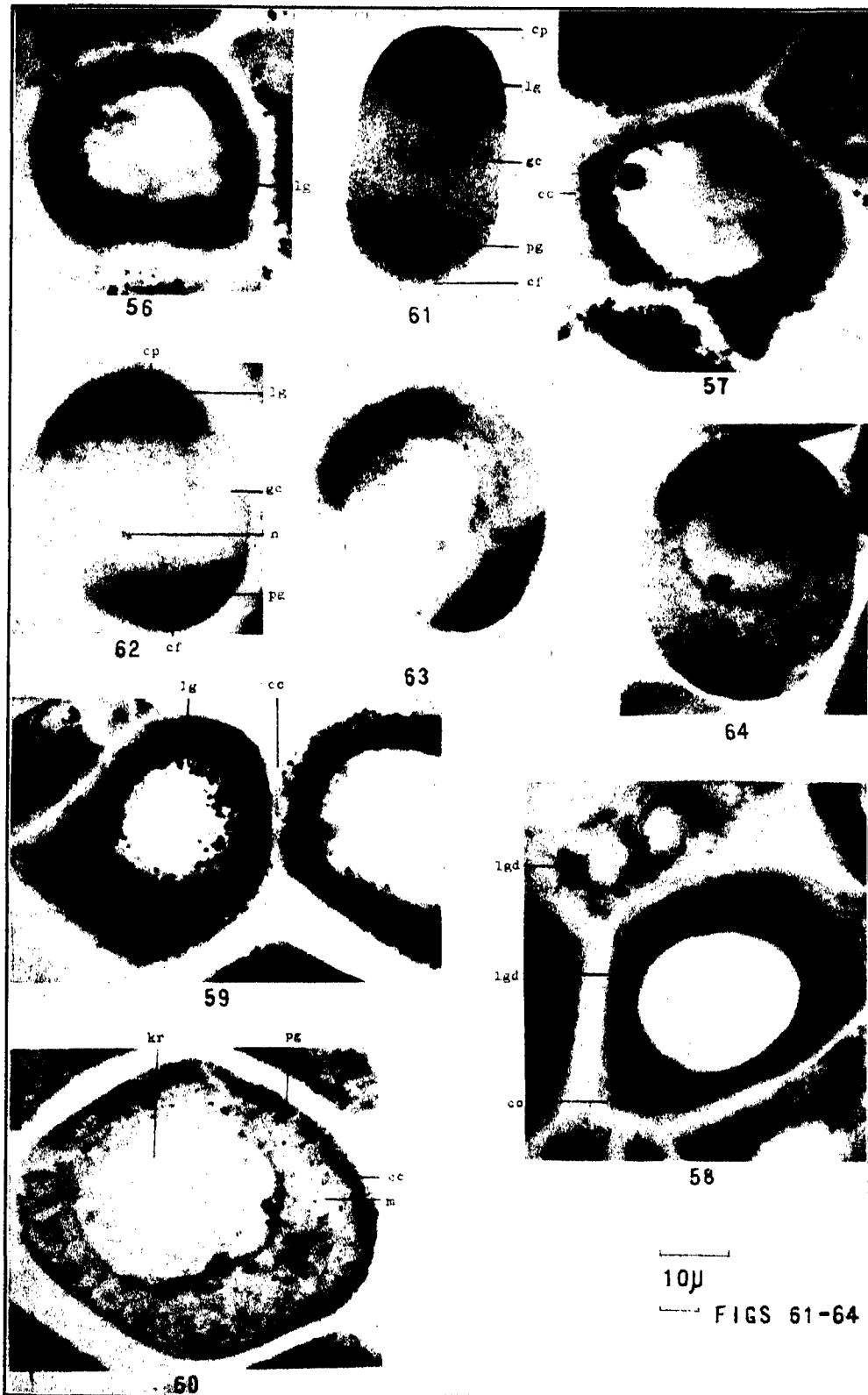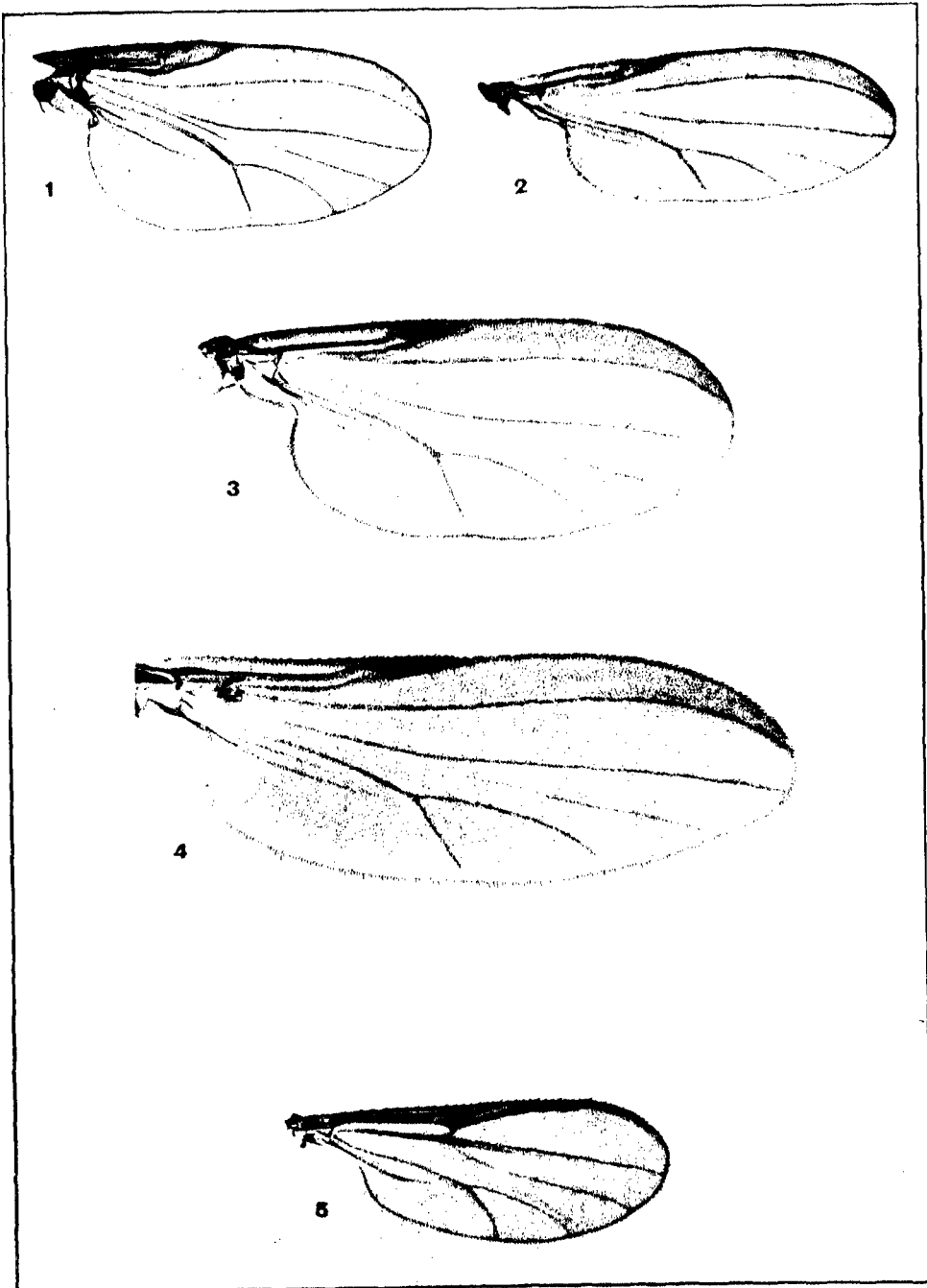
Australasian Ceratopogonidae, Parts II and III.
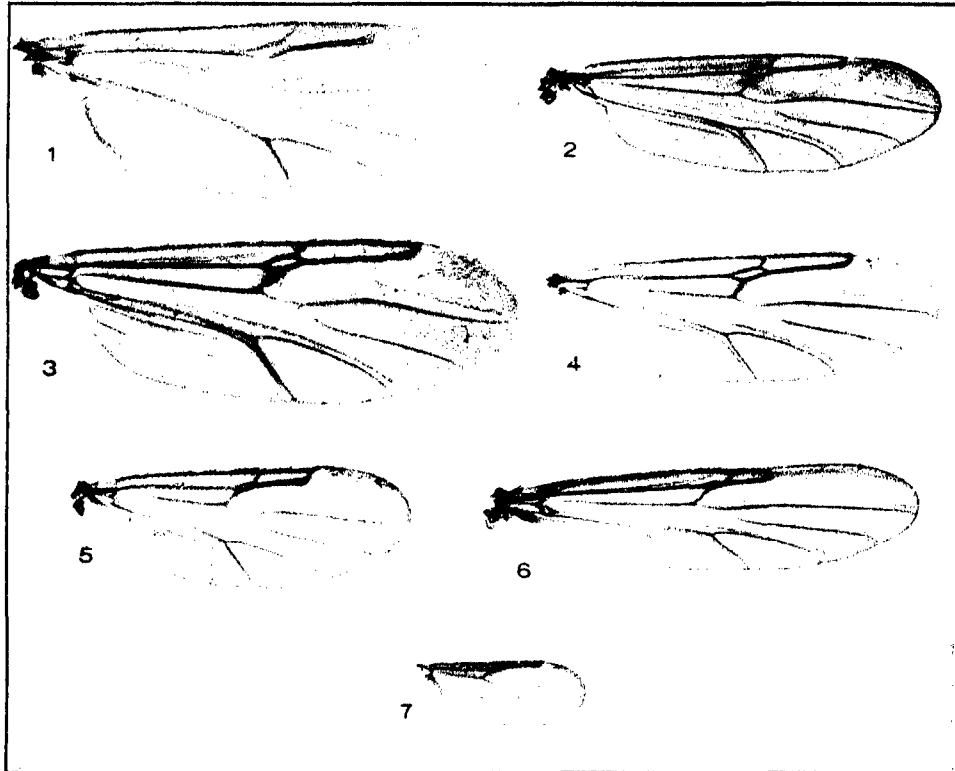
Australasian Ceratopogonidae, Part IV.
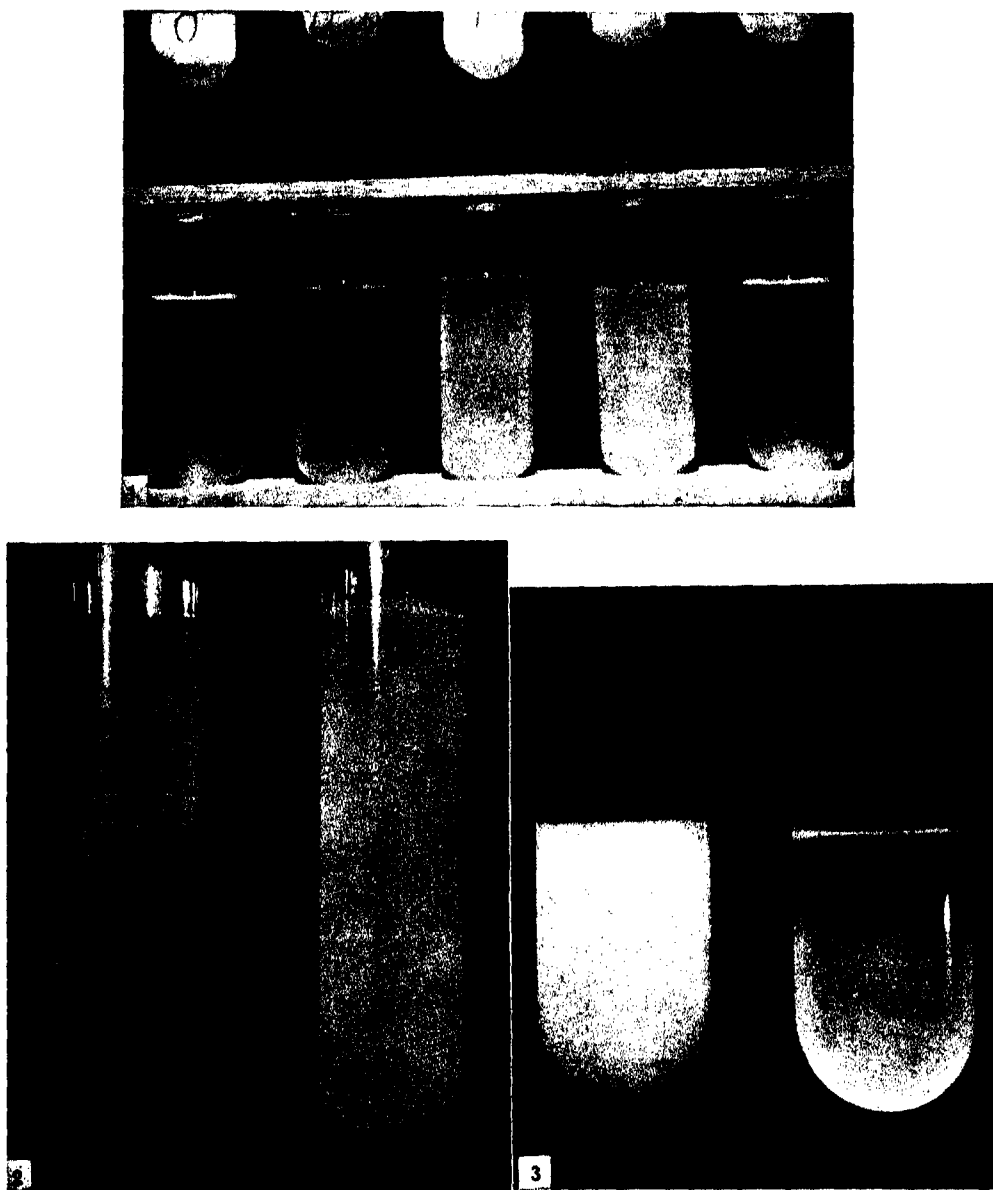
Effect of media on nitrogen-fixation by *Azotobacter indicum.*

A REVIEW OF THE GENUS DENDROBIUM (ORCHIDACEAE) IN AUSTRALIA.

By the Rev. H. M. R. Rupp, B.A., and Trevor E. Hunt.

(Five Text-figures.)

[Read 24th September, 1947.]

In the course of this review we shall have to give a large number of references to botanical publications. With a view to economy of space we are therefore using some abbreviations other than those commonly employed, and we think it will be helpful to set out here a list of the chief abreviations used throughout the paper.

A.O.R.	denotes	*The Australian Orchid Review* (Sydney).
Bail. Q. Fl.	„	Vol. V (only) of F. M. Bailey's Queensland Flora.
Benth.	„	Vol. VI (only) of Bentham's Flora Australiensis.
Bot. Jahrb.	„	*Engler's Botanische Jahrbucher.*
Bot. Mag.	„	*Curtis's Botanical Magazine.*
Bot. Reg.	„	*Edwards's Botanical Register.*
Fedde, Rep.	„	Fedde, Repertorium novarum specierum regii vegetabilis.
Fitzg. A.O.	„	R. D. Fitzgerald's Australian Orchids.
Fitz. ined.	„	R. D. Fitzgerald's unpublished plates in the Mitchell Library, Sydney.
Gard. Chron.	„	*The Gardener's Chronicle* (London).
Journ. Bot.	„	*Journal of Botany* (London).
J. J. Sm.	„	J. J. Smith, Dutch botanist.
Krzl.	„	F. Kranzlin, German botanist.
Fragm.	„	F. Mueller's Fragmenta Phytographiae Australiae.
N.Q. Nat.	„	*The North Queensland Naturalist* (Cairns).
Nov. Guin.	„	Nova Guinea, Orchid Section, by J. J. Smith.
Orch. Alb.	„	Warner and Williams, Orchid Album (London).
Orch. N.G.	„	Schlechter's Orchids of New Guinea (Fedde, Rep.).
Orch. N.S.W.	„	Rupp's Orchids of New South Wales (Sydney).
Orch. Rev.	„	*The Orchid Review* (London).
Pflanz.	„	*Engler's Das Pflanzenreich,* iv, 50, ii, B. 21 (1910).
Proc. R.S.Q.	„	*Proceedings of the Royal Society of Queensland.*
Q.A.J.	„	*Queensland Agricultural Journal.*
Q. Nat.	„	*The Queensland Naturalist* (Brisbane).
R. Br.	„	Robert Brown's Prodromus, 1810 edition.
Rchb. f. Xen.	„	H. G. Reichenbach, Xenia Orchidacea (1858).
Sm. Ex. Bot.	„	Sir J. E. Smith's Exotic Botany (1804).
Sert. Astrol.	„	Voyage of the Astrolabe (Richard).
S.M.H.	„	*The Sydney Morning Herald.*
Wing's S. Sci. Rec.	„	*Wing's Southern Science Record* (Melbourne).

Dendrobium is probably the largest genus in the great family of the Orchidaceae, its only possible rival being Bulbophyllum. It has an extensive distribution, from Japan in the north to Tasmania and New Zealand in the south, and from the foothills of the Himalayas eastward through tropical Asia, Malaya, Indonesia, the Philippines, and most of the islands of the western Pacific. We cannot give an exact statement of the number of known species, but it almost certainly exceeds a thousand. Six hundred have been described from New Guinea alone. Beyond the fact that nearly all are either epiphytes or rock-plants, it is impossible to describe in general terms the multiplicity of forms and habits exhibited by the members of this great group of orchids. Even as concerns the floral structure, there are some species so close to the borderline of other genera that it is difficult to determine their proper position.

In the *Australian Orchid Review* for March, 1942, there appeared a valuable synopsis of the species of Dendrobium known or reputed to occur in Australia. It was contributed

by C. T. White, F.L.S., Government Botanist of Queensland. He enumerates the following 62 plants, but makes it clear that he does not accept all as genuine Australian Dendrobes.

D. Adae	D. dicuphum	D. Jonesii	D. Smilliae
agrostophyllum	Ellen	Keffordii	speciosum
atroviolaceum	elongatum	Keslevenii	striolatum
Baileyi	eriaeoides	Kingianum	Stuartii
Bairdianum	falcorostrum	lichenastrum	Sumneri
Beckleri	Fitzgeraldii	linguiforme	superbiens
bifalce	Fleckeri	monophyllum	Taylori
bigibbum	fuscum	Mortii	tenuissimum
Bowmanii	fusiforme	Muellerianum	teretifolium
Brandtiae	Goldiei	ophioglossum	tetragonum
canaliculatum	Gouldii	Palmerstoniae	Tofftii
Carrii	gracilicaule	Phalaenopsis	undulatum
cucumerinum	Grimesii	Prenticei	variabile
delicatulum	hispidum	pugioniforme	Wilkianum
delicatum	Johannis	rigidum	
	Johnsoniae	Schneiderae	

To these we add the following:

D. ancorarium	D. cancroides	D. Hollrungii	D. luteocilium
antennatum	Foelschei	Nindii	uniflos
aurantiaco-purpureum	gracillimum		

This makes a total of 72. White excludes eight from his list. We delete nine more from the total.

EXCLUDED SPECIES (17).

1. *D. atroviolaceum* Rolfe in *Gard. Chron.* (1890), i, 463, 512. This New Guinea species was reported to have been found some years ago on the Mossman River, N. Queensland. The report has not been confirmed, and there is no real evidence for the occurrence of the plant in Australia.

2. *D. ancorarium* Rupp in *Q. Nat.*, May, 1945. Our reason for rejecting this is discussed in connection with *D. Adae* Bail., q.v.

3. *D. antennatum* Lindl. in *Journ. Bot.* 1843, 236. Given by F. Mueller as an Australian species in his 2nd Syst. Census of Austr. Pl. (1889), but it is a New Guinea plant, and Mueller's record is probably a mistake. He gave no locality, and there are no Australian reports of the species.

4. *D. Bowmanii* Benth. 286. A synonym of *D. Mortii* F. Muell., q.v.

5. *D. Brandtiae* Krzl. in *Gard. Chron.* (1906), 404. Another New Guinea species, for the occurrence of which in Australia there is no evidence. The only remark on its habitat given by Kranzlin is that it "resembles *D. Phalaenopsis, D. bigibbum, D. dicuphum*, and other Dendrobes from North Australia or New Guinea".

6. *D. delicatulum* F. Muell. et Krzl. in *Osterr. Bot. Zeitschr.*, 44 (1894), 162; et Krzl. in *Pflanz.*, 77. Confusion has arisen from the fact that Kranzlin had previously published another species (from New Guinea) under this name, but afterwards suppressed it. Why he and Mueller, still later on, used the name for a different species is not explained. It is this later plant which was supposed to occur in Australia, but the supposition is based on a geographical error of Kranzlin. In the original description the authors make it quite clear that the species belonged to New Guinea, but they had seen specimens "cultivated by colonists at Moreton Bay". Sixteen years afterwards Kranzlin republished the species in *Pflanz.*, l.c. (Mueller was then dead). He says "Neu-Guinea, sudostlicher Teil, Moreton-Bai". Apparently he was under the impression that Moreton Bay was in New Guinea. There is no authentic record for *D. delicatulum* in Australia.

7. *D. Ellen*. As White states, this is an artificial hybrid between *D. Kingianum* (female) and *D. tetragonum*. It was raised by W. Schmidt at Turramurra, N.S.W., and is a most attractive little orchid, but it cannot rank as an Australian species.

8. *D. eriaeoides* Bail. in 2nd Suppl. to *Synopsis Q. Fl.* (1888), et in *Q. Fl.* 1535. R. A. Rolfe removed this plant to the genus *Eria*. (*Orch. Rev.*, xvii (1909), 95.)

In the following year Kranzlin (*Pflanz.*, 249) supported Bailey's view and kept it in *Dendrobium*. Bailey based his determination on the pollinia, which he said agreed both in form and number with those of *Dendrobium*, though he expressed doubts about the final inclusion of the plant in that genus. We had not been able to investigate the matter of the pollinia ourselves, and were prepared to follow Bailey and Kranzlin; but a personal communication from W. H. Nicholls of Melbourne put a different aspect on the subject. Nicholls grew the species in his glass-house for several years; it flowered freely, and he dissected and examined numerous flowers. He sent us copies of his drawings made during these observations. The pollinia are perfectly characteristic of *Eria*; pyriform, 8 in number, arranged in two sets of fours. Either Bailey's specimens must have been abnormal, or he somehow mistook the character of the pollinia. Rolfe's transfer of the plant to *Eria* must be upheld.

9. *D. Foelschei* F. Muell. in *Wing's S. Sci. Rec.* (1882), 230. We regard this as a form of *D. canaliculatum* R.Br., q.v.

10. *D. Fitzgeraldii* F. Muell., in *The Melbourne Chemist*, June, 1884. It is generally accepted that this is conspecific with *D. superbiens* Rchb. f.

11. *D. Goldiei* Rchb. f. in *Gard. Chron.* (1878), 1, 652. A variety of *D. superbiens* with flowers of a richer colour than the type form.

12. *D. elongatum* Cunn. in Lindley, *Bot. Reg.* 1839, Misc. 33. Name invalid. F. Mueller's name *gracilicaule* is the valid name for this species.

13. *D. hispidum* A. Rich. in *Sert. Astrol.*, 13, t. 5. Transferred by Schltr. to the genus *Cadetia*. (Fedde, Rep. i, 1912, 424.)

14. *D. Johnsoniae* F. Muell. in *Wing's S. Sci. Rec.* (1882), 95, et in *Gard. Chron.* (1891), 1, 552. This magnificent orchid was recorded for Cape York by Kranzlin (*Pflanz.*, 260), but he does not say on whose authority, and no other record is known. Bailey did not consider it an Australian species. Mueller originally described it from a specimen sent by the well-known New Guinea missionary, the Rev. James Chalmers, at whose request he named it in honour of a Miss Johnson of Surry Hills, N.S.W. Fitzg. ined., No. 89, with no name attached, undoubtedly represents *D. Johnsoniae*. There is a faint inscription on this plate, "Dinner Island, 28 August, 1888". Now there is a diminutive islet near Mackay, Queensland, bearing that name, but as the result of inquiries we are convinced that no such orchid as *D. Johnsoniae* could ever have grown there. But "Dinner Island" years ago was the name commonly used for the island of Samarai, at the S.E. extremity of Papua. It was certainly known by that name to Chalmers, who had a mission station there. We think it most likely that this was the locality for Fitzgerald's plant. In deleting *D. Johnsoniae* from the list of Australian species, of course we exclude with it the synonyms *D. niveum* Rolfe in *Gard. Chron.* (1891), I, 104, and *D. Macfarlanei* Rchb. f., ibid. (1882), II, 520. Reichenbach's name in any case is invalid, being preoccupied by Mueller for another species.

15. *D. Nindii* W. Hill, in Parliamentary Report of Brisbane Botanic Gardens for 1874. Hill's description is far too inadequate to be accepted for the establishment of a new species. No floral particulars are given beyond the vague remark that there were "eighteen or more large purple, lilac flowers". We can discover no subsequent reference to *D. Nindii* in botanical literature.

16. *D. Taylori* Fitzg., *A.O.* ii, 3. Transferred by Schltr. to the genus *Cadetia*. (Fedde, Rep., l.c.)

17. *D. uniflos* Bail. in *Proc. R.S.Q.*, i (1884), 11. A synonym of No. 16.

Deleting, then, the above 17, we are left with a total of 55 species. Beyond references to the original descriptions, we are unable to supply any information concerning the following six, which do not appear to have been recorded again since they were described.

1. *D. Baileyi* F. Muell. *Fragm.* viii (1874), 173; see also Bail. *Q. Fl.*, 1530.

2. *D. Jonesii* Rendle in *Journ. Bot.*, xxxix (1901), 197. (See *D. gracillimum* below.)

3. *D. Muellerianum* Schltr. in *Fedde, Rep.* iii (1907), 316.

4. *D. Palmerstoniae* Schltr., l.c., 317.

5. *D. Stuartii* Bail. in *Proc. R.S.Q.*, 1 (1884), et in *Q. Fl.*, 1529.

6. *D. Sumneri* F. Muell. *Fragm.* vi (1867), 94. In a personal communication, W. H. Nicholls informs us that he has examined Mueller's type in the Melbourne Herbarium, and cannot distinguish it from *D. bigibbum* Lindl. Bailey omits it from *Q. Fl.* But see Benth., 278, where it is stated to lack the double spur of *D. bigibbum*.

Of the remaining 49 species there are nine which, in our opinion, have been so adequately dealt with in previous publications that we do not feel we can add anything of value to what has been said. We shall therefore only enumerate these species, with references to their bibliography, and brief indications of their habitats. Two special notes, however, are inserted, one under *D. fusiforme* and one under *D. striolatum*.

7. *D. aemulum* R. Br. 333; Benth. 280; Bail. *Q. Fl.* 1527; *Orch. N.S.W.* 117; Fitzg. *A.O.* i, 2; *A.O.R.*, June, 1938, 44 From the Clyde River in southern N.S.W. to the Atherton Tableland in North Queensland.

8. *D. Bairdianum* Bail. in 1st Suppl. to *Synopsis Q. Fl.* et in *Q. Fl.* 1528; Nicholls in *N.Q. Nat.*, July, 1936. Coastal ranges of North Queensland.

9. *D. cucumerinum* Macleay in Lindl. *Bot. Reg.* (1842), Misc. 58; Benth. 283; Bail. *Q. Fl.* 1532; Fitzg. *A.O.* i, 6; *Bot. Mag.* 4619. Open forests E. of the Dividing Range, from Burragorang, N.S.W., to southern Queensland.

10. *D. fusiforme* Bail. *Q. Fl.* 1527; *A.O.R.* Dec., 1939, 114, et June, 1945, 40. N. Queensland coastal and tableland forests.

    Bailey (*Q. Fl.*, l.c.) refers to these PROCEEDINGS, ii (1878), 277, for the original description of *D. fusiforme*. But he did not describe the species there. He recorded it as "a well-marked variety" of *D. speciosum*, mentioning a few of its characteristics; then he added that he *had* supposed it to be a distinct species, and had described it under the name *D. fusiforme*. But he did not say where, if anywhere, such description had been published, nor can we find any reference or allusion to it elsewhere. We consider therefore that "Q. Fl. V, 1527" is the correct citation for the original publication of this species, and that the reference to these PROCEEDINGS should be given only in connection with its synonymy. (*D. speciosum* var. *fusiforme*.)

11. *D. monophyllum* F. Muell. *Fragm.* i (1858), 189; Benth. 282; Bail. *Q. Fl.* 1531; Fitzg. *A.O.* i, 6; *Orch. N.S.W.* 118. Common in scrubs and forests from the Clarence River, N.S.W., northward into the Queensland tropics.

12. *D. pugioniforme* Cunn. in Lindl. *Bot. Reg.* xxv (1839), Misc. 33; Benth. 284; Bail. *Q. Fl.* 1532; *Orch. N.S.W.*, Plate xxi; Fitzg. ined. No. 86. Common in rain forests, especially on mountains, less frequently at lower levels, from southern N.S.W. at least as far north as the Bunya Mountains in Queensland.*

13. *D. rigidum* R. Br. 333; Benth. 284; Bail. Q. Fl. 1533; Fitz. A.O. i, 4. North Queensland forests.

14. *D. striolatum* Rchb. f. in Hamburg. *Gart.* xiii (1857), et in *Xen.* ii, 24, t. 109; Benth. 285; F. Muell., *Key to Syst. Vict.*, Pl. ii, fig. 112; *Vict. Nat.*, Jan., 1938 (a beautiful plate of plants in situ, facing p. 141). From ranges near the South Maitland Coalfields in N.S.W., southwards to eastern Victoria; also in Tasmania, where it is the only species of *Dendrobium*.

We cannot discover the basis for the following record by Bailey in *Proc. R.S.Q.*, 1 (1884), 13: "*D. striolatum* Rchb. f., var. *Beckleri* F.v.M. *Fragm.*, v, 95. Fitzgerald, Part VI." Mueller does not even mention *D. striolatum* in *Fragm.* v (1855-6), though on p. 94 he records it under the name *D. Milligani*, which he subsequently abandoned in favour of Reichenbach's earlier name. On p. 95 he records *D. Beckleri* for the Clarence River, without comment. Actually he had not then published any description of that species, nor did he do so until 1869 (*Fragm.* vii, 59). Below the description he briefly alludes to affinities with *D. striolatum* and *D. Mortii*. Fitzgerald never published

---

* In his article in *A.O.R.*, March, 1947, on the orchids of Cape York, Dr. H. E. Young records *D. pugioniforme* as abundant on the Peninsula; but specimens which he lodged with the Government Botanist at the Brisbane Herbarium have been identified as *D. rigidum* R. Br.

D. striolatum at all, nor does he allude to it in the text accompanying his plate of *D. Beckleri* in *A.O.* I, 7. Whatever be the explanation of Bailey's record cited above, there can be no question that *D. Beckleri* is not a variety of *D. striolatum*, but is a very distinct species of different habit.

15. *D. Tofftii* Bail. in 3rd Suppl. to *Synopsis Q. Fl.* (1890), et in *Q. Fl.* 1524; Fitzg. ined. No. 33; *A.O.R.* Dec., 1941, 82. This very beautiful species is confined to swampy forests along the coastal belt of North Queensland.

Having thus cleared the ground by indicating excluded species, and by enumerating those which, for reasons stated above, we do not propose to discuss further, we are now in a position to proceed with our review of the remaining 40, viz.:

D. Adae	*D. dicuphum*	*D. Keffordii*	*D. Schneiderae*
agrostophyllum	*falcorostrum*	*Kestevenii*	*Smilliae*
aurantiaco-	*Fleckeri*	*Kingianum*	*speciosum*
purpureum	*fuscum*	*lichenastrum*	*superbiens*
Beckleri	*Gouldii*	*linguiforme*	*tenuissimum*
bifalce	*gracilicaule*	*luteocilium*	*teretifolium*
bigibbum	*gracillimum*	*Mortii*	*tetragonum*
canaliculatum	*Grimesii*	*ophioglossum*	*undulatum*
cancroides	*Hollrungii*	*Phalaenopsis*	*variabile*
Carrii	*Johannis*	*Prenticei*	*Wilkianum*
delicatum			

16. D. ADAE Bail. in *Proc. R.S.Q.*, i (1884), et in *Q. Fl.* 1539; Rupp in *Q. Nat.* May, 1945, Plate vi, et ibid., May, 1946, 12. This dainty species, with creamy-white flowers, tomentose labellum, and an exquisite perfume, deserves more attention from orchid growers than it has yet received. Though a native of tropical Queensland, it thrives and flowers well under ordinary bush-house conditions, as far south as Sydney. Recently it was the subject of an article by Rupp (see last citation above) suggesting that it is a dimorphic species. In the preceding year the writer had described what he believed to be an allied (but distinct) species from Mount Spurgeon, in the Mossman area of North Queensland, under the name *D. ancorarium*—in allusion to a curious anchor-like device at the foot of the column (*Q. Nat.*, May, 1945). The flowers were pale-green and scentless, and the labellum was glabrous. Next year this plant (a young one) bore two racemes. In one the flowers were almost exactly as described for the new species; but in the other, which opened later, they were in every respect typical flowers of *D. Adae*. It is for this reason that we have put *D. ancorarium* into our list of excluded species. We should be glad to hear from anyone who has observed this peculiarity in connection with *D. Adae*.

17. D. AGROSTOPHYLLUM F. Muell. *Fragm.* viii (1872), 28; Benth. 281; Bail. *Q. Fl.* 1529; Krzl., *Pflanz.* 158; Fitzg. *A.O.* ii, 3. This is one of the few instances where Fitzgerald's plate does scant justice to its subject. It shows half-closed flowers of a dull and unattractive yellowish tint, and it would appear that his specimen was in very poor condition. Actually the flowers expand widely, and are a brilliant canary-yellow. The labellum is relatively large, and very conspicuous in the fully-expanded flower. Though the individual flower is small, the bright colour of the racemes, and their pleasing perfume, make this quite an attractive species. Like *D. Adae*, although a native of tropical Queensland, it is amenable to ordinary bush-house conditions in much cooler climates. (Text-fig. 1.)

18. D. AURANTIACO-PURPUREUM Nicholls in *N.Q. Nat.*, March, 1942. This is one of several very diminutive North Queensland orchids which present peculiar difficulties to the taxonomist. All are closely related, and all seem to be very near the hypothetical borderline separating *Dendrobium* from *Bulbophyllum*. Two of them, *D. lichenastrum* and *D. Prenticei*, were described by Mueller as species of the latter genus, although in the case of *D. lichenastrum* he evidently suspected that it might be a Dendrobe. Fitzgerald, in *A.O.* ii, 5, figures a plant over the name *B. lichenastrum*, which is quite irreconcilable with Mueller's type specimens in the Melbourne Herbarium. Nicholls, in an attempt to clarify the position of these small orchids in *N.Q. Nat.*, Sept. and Dec., 1938, identified the plant of Fitzgerald's plate with an undescribed

species which he had received from North Queensland, and which he named *D. variabile.* Subsequently, however, a different plant was sent to him, which he considered to be definitely that figured by Fitzgerald; and to this he gave the name of *aurantiaco-purpureum.* While we do not question this later determination, and agree with Nicholls in placing these plants in *Dendrobium,* we must confess to a hope that he will give us a revision of his exposition of the whole group, for we find it very difficult, in examining living material, to distinguish between his species. Moreover, we do not think he was justified in making the absence of a definite pseudobulb a ground for deciding against *Bulbophyllum* as the proper genus for these plants. The Himalayan *B. hymenanthum* Hook. and *B. gracilipes* King and Pantl.; the Malayan *B. botryophorum* Ridl. and other species that could be cited, are quite bulbless. Our agreement with his decision in favour of *Dendrobium* is based upon the floral characters rather than upon the habit of the plants. (Text-fig. 3, A.)

Text-fig. 1.—*Dendrobium agrostophyllum.* Inset (right): Upper surface of labellum (enlarged).

Text-fig. 2.—*Dendrobium Keffordii.* A. A lateral sepal (enlarged) twisted in the corkscrew form described in the text. B. Two flowers a few hours after expansion. C. Upper surface of labellum (enlarged). D. A plant (reduced).

Text-fig. 3.—Flowers of four diminutive north Queensland species of *Dendrobium* (side view, front view, upper surface of labellum shown for each species. All figures enlarged).
A. *D. aurantiaco-purpureum.* B. *D. lichenastrum.* C. *D. variabile.* D. *D. Prenticei.* (After plates by W. H. Nicholls.)

19. D. BECKLERI F. Muell. *Fragm.* v (1865), *nomen* et ibid., vii (1869), 59; Fitz. *A.O.* i, 7; Bail. *Q. Fl.*, 1534; *Orch. N.S.W.*, 120. Bentham suppressed this species, but as Fitzgerald and others have pointed out, he evidently misinterpreted the material available to him. Actually he describes *D. Beckleri* under the name *D. Mortii,* q.v. *D. Beckleri* is a very well-marked species, the principal of those popularly called "Pencil Orchids", from the shape of their leaves. A form with mauve flowers has been recorded in northern N.S.W.

The species is found chiefly in open forest country, from the Hunter Valley in N.S.W. northward into the Queensland tropics.

Var. *racemosum* Nicholls in *N.Q. Nat.*, June, 1936. A North Queensland form with a very definite racemose inflorescence. In the type form, although the flowers are numerous, they are solitary.

20. D. BIFALCE Lindl. in *Journ. Bot.* ii (1843), 237; Krzl., *Pflanz.* 252; Rupp in *N.Q. Nat.*, Sept., 1945. White admits this as an Australian plant from its occurrence on the island of Saibai, politically part of Queensland, but geographically belonging rather to Papua. However, it was collected by R. L. Hunter in June, 1945, in the Portland Roads area north of Cairns. It is surprising that so conspicuous a species remained undiscovered on the mainland for so long. It has a wide range of habitat, extending from New Guinea to Fiji, where the type was found. A fuller description than Lindley's is given in *N.Q. Nat.*, loc. cit.

21. D. BIGIBBUM Lindl. in Paxton, *Flower Garden*, iii, 25 (1852), fig. 245; Krzl., *Pflanz.* 260; Benth. 277; Bail. *Q. Fl.* 1523; Fitzg. *A.O.* ii, 5; *Orch. Alb.* I, t. 38 (1882); *Bot. Mag.*, t. 4898.

We find it necessary to associate with this species No. 44, D. PHALAENOPSIS Fitzg. in *Gard. Chron.* (1880), ii, 38, et ibid. (1886), ii, 556, fig. 110, et in *A.O.* i, 7; Krzl., *Pflanz.* 261; *Orch. Alb.* iv (1885), t. 187; *A.O.R.* March, 1938 (frontispiece). We have given much time and thought to the vexed problem of the relations between these beautiful North Queensland orchids. We realize that the conclusion we have at last reached will probably be unacceptable to some of our readers, and that it will disappoint many who have been anxious to see a concise and clear statement of the distinctions between the numerous varieties (of both *D. bigibbum* and *D. Phalaenopsis*) which from time to time have been recorded. But we have become convinced that Bailey was entirely correct, from the botanical standpoint, when he reduced Fitzgerald's *D. Phalaenopsis* from specific rank to the status of a variety of *D. bigibbum* (*Q. Fl.*, loc cit.). We may assume, we think, that Fitzgerald has faithfully depicted the typical *D. Phalaenopsis* in *A.O.* i, 7, and the typical *D. bigibbum* in *A.O.* ii, 5. No one examining these plates can deny that there are differences between the two orchids figured there; *but are they in any respect more important* than those which distinguish type from variety in scores of other species? Lest this be thought too vague a comparison, take two of our own Australian species of this same genus, viz., *D. teretifolium* and *D. tetragonum*. In what particulars are the differences between *D. bigibbum* and *D. Phalaenopsis* more striking, or more important botanically, than those between the typical *D. teretifolium* and its tropical variety *fasciculatum*? or those between the little sober-hued flower of the typical *D. tetragonum* and the large and colourful flower of var. *giganteum*? Even in their recognized varieties, *D. bigibbum* and *D. Phalaenopsis* seem to approach one another. White's var. *compactum* is generally considered a very distinctive form of the latter; but in what respects does it differ from Reichenbach's *D. bigibbum* var. *superbum*?

Generally speaking, the flowers of *D. Phalaenopsis* are superior, both in dimensions and in depth of colour, to those of *D. bigibbum*. But size and colour cannot be made the criteria for specific separation. It is the morphology of the flower which counts most; and we are satisfied that the structural differences between the flowers of these plants are very slight, and even at their best, are not of much botanical importance. Differences in dimensions, colour-scheme, and precise shade of colour itself may conveniently be used to denote the distinctive appearance they give to this or that variant from the typical form; but not to establish new species. If this point of view is not accepted, why should we not split both *D. bigibbum* and *D. Phalaenopsis* into still more species? The differences between the typical *D. Phalaenopsis* (the "Cooktown Orchid", as it is called) and its variety *Rothschildianum*, or the new variety *W. Parton*, seem to us greater than those which are supposed to distinguish it from *D. bigibbum*. We follow Bailey in regarding *D. Phalaenopsis* as a large and beautiful form of *D. bigibbum*, itself even more subject to variation than the species proper; and we think that its named varieties should be reduced to sub-varieties. We may be accused of inconsistency in holding these views, yet still retaining both names in our list of species. We do this because we recognize that the *bigibbum-Phalaenopsis* problem is a very difficult one, and that

others who are as well qualified to judge as we are, may uphold the view that here are two distinct species. We are unable to endorse the view ourselves.

We do not think that in a review such as this we can enter into a discussion of the many varieties which have been published in connection with *D. bigibbum* and *D. Phalaenopsis*. Most of them are based on differences in the colour-scheme of the flowers; in a few there are other distinctions, such as dwarf and compact habit, etc. These variations are chiefly of interest to orchid growers, and would be more appropriately discussed in a journal exclusively devoted to orchid cultivation. We may add that in any such discussion we think a third species, *D. dicuphum* F. Muell., should receive some consideration. At least one form of this species approaches very closely *D. bigibbum* var. *candidum*.

D. bigibbum is found chiefly in the Cape York Peninsula, but is occasionally seen a good deal to the south of that area. The vernacular name so commonly used for var. *Phalaenopsis*—"Cooktown Orchid"—gives the clue to its principal habitat, though it is by no means exclusively confined to the Cooktown district. With its large purple flowers, usually shading to deep mauve on the labellum, it is one of the most beautiful of all Australian orchids, and can hold its own even among the most highly valued species of exotic origin.

22. D. CANALICULATUM R. Br. 333; Benth. 282; Bail. *Q. Fl.* 1530; Fitzg. *A.O.* i, 3; *Bot. Mag.* 5537 (as *D. Tattonianum*). Syn. *D. Tattonianum* Bateman in *Gard. Chron.* (1865), 890. Another very attractive species from North Queensland, extending to the Northern Territory. It is far more variable than the descriptions indicate, although Bailey in a footnote remarks, "colouring and marking very variable". The contour of the labellum is remarkably inconstant, ranging from almost orbicular to elongate-rhomboid. The general habit of the plant is also variable. In the commonest form the pseudobulbs are very short and greatly swollen, prompting the vernacular name "Onion Orchid"; but sometimes they are longer and not conspicuously swollen. The leaves, too, are sometimes very thick and deeply channelled, sometimes very slender and almost terete, with only an obscure median channel. In 1882 Mueller, in *Wing's S. Sci. Rec.*, p. 230, described a Dendrobe from the Northern Territory as *D. Foelschei*. He remarked upon its affinity with *D. canaliculatum*, but thought that it merited specific rank. By the courtesy of the authorities of the Victorian National Herbarium, we have been able to examine flowers of the type specimen. We think Kranzlin was right (*Pflanz.* 274) in reducing *D. Foelschei* to a form of *D. canaliculatum*; although W. H. Nicholls is inclined to support Mueller. But the flowers differ no more strikingly from the typical *D. canaliculatum* than do others generally accepted as only variants. Since, however, this plant appears to *combine* several variations, we think it may be retained as a named variety.

Var. *Foelschei*, n. var. (*D. Foelschei* F. Muell., loc. cit.). Pseudobulbs not swollen, or slightly fusiform; leaves very slender, nearly terete. Flowers smaller, or at least more attenuated, than in the type, the mid-lobe of the labellum more or less rhomboid—Northern Territory. (Flowers of a plant collected by R. J. Langdon (of Adelaide), near Darwin, appear to belong to this form, though the floral segments are longer than in Mueller's plant.)

Var. *nigrescens* Nicholls in *A.O.R.* Sept., 1942, frontispiece and p. 40. Perianth-segments pale green towards the base, deep sepia-brown above; labellum white with the usual purple markings. Locality doubtful. This seems to be the form recorded on the Cape York Peninsula by Dr. H. E. Young in *A.O.R.*, March, 1947.

23. D. CANCROIDES Hunt in *N.Q. Nat.*, June, 1947. This is a recent discovery by J. H. Wilkie in the Bellenden Ker Range, North Queensland. As in the case of *D. bifalce*, it is surprising that so large and distinctive a species should have escaped detection for so long. The curious, reddish-brown flowers, which do not expand widely, somewhat resemble small crabs. The species seems to be closely related to the New Guinea *D. Gjellerupii* J. J. Sm.; its nearest Australian relative is *D. luteocilium* Rupp.

24. D. CARRII Rupp and White in *Q. Nat.* March, 1935, 61, and Feb., 1942, 19. A small plant with the habit of *D. monophyllum*, F. Muell., but the pseudobulbs are never crowded, and the flowers are white or cream, with narrow sepals and petals; lateral lobes of the labellum splashed with red, mid-lobe yellow. Mount Spurgeon, on the main coast range behind Mossman, north Queensland.

25. D. DELICATUM Ball., *Q. Fl.* 1527; Krzl., *Pflanz.* 271; Rupp, in *Q. Nat.* March, 1935, 61; Weinthal in *A.O.R.* June, 1939. Syn. *D. speciosum* Sm. var. *delicatum* Ball. in *Proc. R.S.Q.*, 1 (1884). Probably few Australian orchids have been subjected to more argument and discussion than this. For those who wish to follow the inquiries into its identity, its status, and its relation to *D. Kestevenii* Rupp, we cite the following additional references: these PROCEEDINGS, lviii, Parts 3, 4 (1933), 223; *A.O.R.*, Dec., 1939, 124; Rolfe in *Orch. Rev.*, April, 1908. An admirable photograph will be found in *A.O.R.*, March, 1940, p. 20.

It now seems practically certain that the origin of *D. delicatum* lies in natural hybridization between *D. speciosum* and *D. Kingianum*. The English experiment in crossing these, mentioned by Rolfe, l.c., was not accepted in Australia as conclusive, because there was some doubt whether English botanists had not previously mistaken the white-flowering form of *D. Kingianum* for *D. delicatum*. But more recently this experiment was repeated by Dr. H. E. Young of Brisbane, and the resulting hybrid cannot be distinguished from *D. delicatum*. In the wild state, however, the latter is a very variable plant, and several of the forms may have originated independently (*A.O.R.* Dec., 1939, l.c.). But, granted the hybrid origin of *D. delicatum*, does this necessarily imply, as assumed by Rolfe, its disqualification as a species? If so, then there must be thousands of other plants whose specific rank rests solely upon the fact that their hybrid origin lacks the demonstration which has been given in this case—surely a rather precarious foundation. Lotsy long ago showed us what a large part hybridization has played in the evolution of species. If a natural hybrid is established independently of its "parents", and reproduces itself without exhibiting the slightest tendency to revert to the character of either parent, surely it is entitled to specific rank.

A very curious point in connection with *D. delicatum* is the limited area of its habitat. It was first found on the main Dividing Range near Toowoomba; more recently it has been collected or recorded in a few other southern Queensland localities. Now *D. speciosum* and *D. Kingianum* occur together, often in abundance, along the whole coastal belt of northern New South Wales for several hundred miles. Yet no plant suggesting hybridization between them has been found on the New South Wales side until Bullahdelah is reached, some 350 miles in a direct line from the *delicatum* area. Diligent search has been made in many localities, without result. At Bullahdelah a plant which somewhat resembles *D. delicatum*, and is probably of similar origin, was discovered some years ago, and received the name *D. Kestevenii*. Why neither of these plants should occur in that long gap between them is something of a mystery.

26. D. DICUPHUM F. Muell. *Fragm.* viii (1872), 28; Benth. 277; Rupp and Nicholls in *N.Q. Nat.* Sept., 1943. A common species in the Northern Territory and recorded by Gardner in the N.W. of Western Australia. The plate by Nicholls in *N.Q. Nat.* shows the typical form; but another was collected (independently) by G. L. Piper of Brisbane and R. J. Langdon of Adelaide, when on active service in the Territory. We are naming this var. *grandiflorum*, but we confess we can see little to distinguish it from *D. bigibbum* var. *candidum*. Undoubtedly *D. bigibbum* and *D. dicuphum* are closely allied; but as no other form of *bigibbum* is recorded from the *dicuphum* area, we attach this variety to the latter.

Var. *grandiflorum*, n. var. *Flores majores, nivei.* Flowers half as large again as those of the type form, pure white.

27. D. FALCOROSTRUM Fitzg. in *S.M.H.*, Nov. 18, 1876, et *A.O.* 1, 5; *Orch. N.S.W.*, 116; see also *A.O.R.*, March, 1937, 17; ibid., Dec., 1937, 11. This beautiful species is

well known to orchid growers under the name "Beech Orchid". Questions in regard
to its habitat are frequently raised, and we are prepared to give a definite answer.
It has never been found except in forests of the Antarctic or Negrohead Beech
(*Nothofagus Moorei*). The southern limit of this tree is on the south side of the
fall from the Barrington Tops plateau, some 60 miles N. of Newcastle, New South
Wales. It occurs again about Dorrigo, on the eastern side of New England, and
extends sparingly from there to the Lamington National Park in the Macpherson
Ranges of southern Queensland. It is rarely seen at an elevation of less than
3,000 ft. Before the march of settlement had destroyed the greater part of the
Dorrigo beech forests, *D. falcorostrum* grew there literally in thousands; today it
is in danger of extinction. Although it is confined to the beech forests, within them
it occurs on other trees besides the beeches, being often found on the Mountain
Wattle (*Acacia elata*). It is easily cultivated, and as a rule blooms most prolifically.
Being a large and robust plant, it makes a fine display with its masses of snowy
white flowers, which are intensely fragrant during the warmer hours of the day.
We have seen plants bearing over 100 racemes.

28. D. FLECKERI Rupp and White, *Q. Nat.*, Feb., 1937; Rupp in *N.Q. Nat.*, Dec., 1937. A
very dainty species from the Upper Mossman River jungle near Mount Spurgeon,
north of Cairns. When not in bloom, the plant might easily be mistaken for
D. Adae, though less robust; but the flowers are very different. They are of
moderate size, and of a rich apricot colour; the labellum is densely pubescent, with
purplish-red markings. Like *D. Adae*, this species is quite amenable to ordinary
bush-house conditions, even in much cooler climates than that of its native habitat.

29. D. FUSCUM Fitzg. in *S.M.H.*, Sept. 24, 1879, et *Gard. Chron.* (1879), II, 680; also Fitzg.
ined. No. 83. Fitzgerald's locality note merely gives "North Queensland". The
species has been collected by J. S. Edgar at Port Denison. It is apparently rare.
A robust plant up to 90 cm. high, with slightly fusiform stems bearing leaves on
the upper portions only. Flowers about 12; sepals about 2 cm. long, red-brown with
lighter edges, not undulate; petals longer, darker, undulate in the upper half;
labellum half as long as the petals, linear, lateral lobes incurved, mid-lobe minute,
longitudinal calli of the disc 5. The species appears to be closely related to
D. undulatum R. Br.

30. D. GOULDII Rchb. f. in *Gard. Chron.* (1867), 901, et in *Xen.* ii, 167, t. 169; J. J. Sm.
in *Nov. Guin.* viii, 67, t. xxiii; Krzl., *Pflanz.*, 155. Little is known of this species in
Australia. Reichenbach's description is meagre. He records a variety, var. *acutum*,
and it is this which is believed to be an Australian plant; but J. J. Smith, who gives
the record "Thursday Island" for the species, says nothing of the variety. Reichen-
bach merely says that *D. Gouldii* is one of the numerous "Polynesian" discoveries of
John Gould Veitch, in whose honour he named it. In the Sydney Herbarium there
is a specimen, collected by someone unknown at Thursday Island in 1897, which
Rupp considers to be this species, though he found it labelled *D. Johannis*. The
flowers are much larger than those of the latter, and the labellum agrees almost
perfectly with Smith's figure, loc. cit.

31. D. GRACILICAULE F. Muell. *Fragm.* 1 (1859), 179; *A.O.R.*, Sept., 1940, 72; Fitzg. ined.
Nos. 22, 23. Syn. *D. elongatum* Cunn. (not of Lindl.); *D. brisbanense* Rchb. f.
Formerly very common in many coastal forests of N.S.W., but now chiefly found
north of Port Jackson. Extends to tropical Queensland; also in Lord Howe Island.
The plant varies in height from 25 to 90 cm. Stems very slender. Racemes short,
in the type form with small, fragrant yellowish flowers more or less blotched outside
with red-brown.

Var. *Howeanum* Maiden in these PROCEEDINGS, Part 3 (1889), 382. This is the
Lord Howe Island form; but some years ago a plant apparently identical with it was
collected by Dr. C. H. Jaede at Mangrove Mountain near Gosford, N.S.W. The
flowers are a rich creamy-yellow without any blotches; they have a different
perfume; and there is a greater development of leaves.

32. D. GRACILLIMUM Rupp, *Vict. Nat.* lxi (1945), 200. Syn. *D. speciosum* Sm. var. *gracillimum* Rupp in these PROCEEDINGS, liv (1929), 550, et *Orch. N.S.W.*, 114; *A.O.R.* June, 1940, 63. This plant resembles a very robust *D. gracilicaule*, but the flowers are far more like those of *D. speciosum*, except that the perianth-segments are barely half as long as in the latter. In all probability it originated as a natural hybrid between these species. Flowers vary in colour from white through cream to deep yellow. It is thought that the white-flowered form may be identical with Bailey's *D. speciosum* var. *nitidum* (*Proc. R.S.Q.*, i (1884)), and a further suggestion has been made that Rendle's *D. Jonesii* (see No. 2 above) is the same plant. Bailey gives "Tropical Queensland" as the habitat of his var. *nitidum*. Nothing resembling it has been seen by us from that area, although it has been looked for. But his description does agree fairly with the white *D. gracillimum* of southern Queensland and northern N.S.W. Unfortunately there are no certified specimens of var. *nitidum* in existence. Rendle's *D. Jonesii* was named from a plant sent to England from Innisfail in North Queensland, which flowered in Surrey in 1899. His description agrees very well with the *cream*-flowered *D. gracillimum*. But we have seen no plant from tropical Queensland which could possibly be determined as this species. We do not question the occurrence of either *D. speciosum* var. *nitidum* or *D. Jonesii* in the areas recorded by Bailey and Rendle; but we think actual specimens are required in order to determine whether they are identical with each other and with *D. gracillimum*. Until this point is settled, the last-named species must be allowed to stand.

33. D. GRIMESII White and Summerhayes in *Kew Bulletin* No. 3, 1934, p. 106. The affinities of this rare species are with *D. teretifolium* R. Br., to which it bears a considerable resemblance. The leaves are thicker, and the floral characters differ in important respects. The sepals and petals are shorter, and the former are 3-nerved, not 5-nerved. The mid-lobe of the labellum is marked by 5 sub-parallel longitudinal veins, but is completely devoid of lateral veins at right angles to them. The species has only been found at Lake Barrine on the Atherton Tableland, in north Queensland.

34. D. HOLLRUNGII Krzl. in Schumann and Hollrung, *Fl. Kais. Wilh. Land* (1889), 32. The only form in which this plant is known to occur in Australia is var. *australiense* Rendle, *Journ. Bot.* xxxvii (1899), 339. Rendle's type was collected at Innisfail, north Queensland, and sent to England, where it flowered at Ewhurst, Surrey, in 1899. In 1946 Hunt received a plant collected by Mrs. Eunice Kirkwood at El Arish, Cairns district, which flowered in October. This is the only record since Rendle's description was published. *D. Hollrungii* is closely related to *D. Smilliae* F. Muell., and the Australian form may perhaps have been occasionally mistaken for that species. The flowers are a dead, waxy white, tipped with shining green, and having some crimson markings on the column. They are in a conical cluster on short, erect racemes. Bailey mentions Rendle's variety in his "Comprehensive Catalogue of Queensland Plants", 1909. We include this plant under the name given to it by Rendle; but we venture to suggest that further investigation may show the desirability of transferring it to *D. Smilliae*. So far as we can judge, there is nothing in its character which would debar it from inclusion within Mueller's species; and it seems to us far more likely that it had its origin in variation from this Australian orchid (which occurs in the same area), than from a species of an area in the north-western parts of New Guinea.

35. D. JOHANNIS Rchb. f., *Gard. Chron.* 1865, 890, et *Xen.* ii, 165; Benth. 279; Bail. *Q. Fl.* 1525; *Bot. Mag.* t. 5540. This species is obviously related to *D. undulatum* R. Br., but is a much smaller plant. It varies considerably, but so far as we know only one variety has been named. In a form from the Torres Strait islands represented in the N.S.W. National Herbarium, the perianth segments are relatively very broad; and a specimen in Rupp's collection there, collected by Goadby near Cairns (possibly in cultivation), has very large flowers. The typical form is multi-coloured;

a rich brown is predominant, but yellow, green, and red tints are frequent. The species is found chiefly in the far north of Queensland along the Cape York Peninsula, extending to the Torres Strait islands.

Var. *semifuscum* Rchb. f., *Gard. Chron.* 1883, 268. Petals pale brown. Cooktown, north Queensland.

36. D. KEFFORDII Bail., *Proc. R.S.Q.* i (1884), et *Q. Fl.* 1530. The opinion has been expressed by some botanists that this plant and *D. Baileyi* F. Muell. are conspecific. As indicated above, we have not been able to obtain specimens of *D. Baileyi*, and are therefore not in a position to state any view of the relations between these two. But we wish to point out: (1) that Bailey himself discovered the plant which Mueller, in 1874, named after him; and (2) that Bailey named and described *D. Keffordii* ten years later. We think it extremely unlikely that a botanist of his calibre could be so forgetful of the plant which bore his own name, as to describe it under another name.

A fine plant of *D. Keffordii* was received by Rupp in 1946 from Cape Tribulation, 50 miles north of Cairns (coll. W. W. Mason Jun.). It flowered in February, 1947, and from the observations made since its arrival, we submit the following description supplementary to that given by Bailey. (Text-fig. 2.)

Stems of wiry texture, no thicker than that of a fishbone fern (*Nephrolepis*), numerous. Leaves linear-lanceolate, unequally and very minutely emarginate at the tips; dimensions very variable, but those given by Bailey are rather above the average. Flowers in pairs, yellowish-green outside with a few dark spots or streaks, inside densely speckled with dark reddish-purple dots; perianth segments all filiform, the newly opened flowers resembling those of *D. tetragonum* var. *Hayesianum*. Disc of the labellum with a single rather broad longitudinal callus, more or less channelled along the lower portion, widening about the junction of the lateral lobes, and almost covering the surface of the mid-lobe inside its fringed margins, but not reaching the apex. Within a few hours after the expansion of the flowers, the filiform sepals and petals begin to curve inwards and to twist like miniature corkscrews, finally becoming entangled round the labellum and column. The flower remains alive in this curious tangle for several days before withering. In none of the flowers observed was the process just described due to pollination, for every anther remained intact throughout. Is it possible that in its native habitat the flower is quickly visited by some pollinating agent, and has developed this tangling process to prevent further interference with the gynostemium? It may reasonably be objected that if the flower is *not* pollinated, the stimulus required for the process would be lacking. But what other explanation can be suggested?

D. Keffordii is found in the mangrove scrubs of the North Queensland coast. Kranzlin, in *Pflanz.* 174, gives as a synonym *D. Armitiae* Bail. (*Q.A.J.* iv (1899), 48); but we cannot endorse this. Bailey's description of *D. Armitiae*—from New Guinea—implies floral characters which we regard as irreconcilable with those of *D. Keffordii*.

37. D. KESTEVENII Rupp, in these PROCEEDINGS, lvi (1931), et ibid., lviii (1933), 223, et in *Orch. N.S.W.*, 114, et in *A.O.R.*, Dec., 1939, 124. Reference has already been made to this species under *D. delicatum*, to which it is obviously closely allied. The pseudobulbs of *D. Kestevenii* are more consistently robust, and of a paler green; the racemes are stronger and more erect; and the flowers do not expand so widely. The only named variety has no counterpart in the variations from the type of *D. delicatum*. Both species and variety appear to be confined to the Bullahdelah district, north of Port Stephens, N.S.W.

Var. *coloratum* Rupp, in *Orch. N.S.W.*, l.c. Stems dwarf, very crowded, curved. Flowers mottled and suffused with rosy pink. Petals almost acuminate.

38. D. KINGIANUM Bidw. in Lindl., *Bot. Reg.* (1844), Misc. 11; ibid. (1845), t. 61; *Bot. Mag.* 4527; Benth. 280; Bail. *Q. Fl.* 1528; *Orch. N.S.W.*, Plate xx. This variable species is favoured by growers for its bright colour, its pleasing perfume, and its

easy cultivation. It is essentially a rock orchid, growing freely, often in extensive masses, on ledges or in crevices of cliffs, or sometimes covering the whole face of a rock. In view of its hardy nature and its abundance in many localities, its range of habitat is surprisingly restricted. We have no definite record of its occurrence south of Port Stephens in N.S.W. From there it extends northward as far as the Glasshouse Mountains in southern Queensland. The plants vary greatly in dimensions, often exceeding 40 cm. in height, but just as often reaching only 12 cm. Flowers on the dwarf plants are as large as those of the tall form. They vary in colour from pure white (rare) through several shades of pink and purple, to deep mauve. The named varieties are:

Var. *pallidum* Bail. in *Proc. R.S.Q.* 1 (1884). Stems weak, up to 22 cm. high. Racemes with very pale lilac flowers.

Var. *Silcockii* Bail., *Q. Fl.*, l.c. Stems robust, light green, up to 35 cm. high. Flowers white with a purple labellum.

Var. *Aldersoniae* Bail. in *Q.A.J.* xv (1905), 781. Flowers white, pale purple spots on the sepals, and pale purple labellum.

Var. *pulcherrimum* Rupp in *Orch. N.S.W.*, 116. Stems crowded, usually dwarf but robust; flowers deep mauve.

D. Kingianum exhibits a tendency to produce aerial growths more freely than any other Australian species. These often flower before dropping from the parent plant. The form with pure white flowers is generally regarded as an albino. It occurs sporadically wherever the species is found, and has occasionally been mistaken for *D. delicatum*, but the latter is a much larger plant, with pink tints in the flowers.

We cannot agree with Kranzlin in reducing *D. subquadratum* J. J. Sm. to a variety of *D. Kingianum* (*Pflanz.* 274). Not only is it extremely unlikely that a variety of the latter should occur in New Guinea, more than 1,500 miles from the Glasshouse Mountains; but the floral details of *D. subquadratum* as shown by Smith in *Nov. Guin.* viii are very different from those of *D. Kingianum*.

39. D. LICHENASTRUM F. Muell. *Fragm.* vii (1869), 60 (nomen); Krzl., *Pflanz.* 289; Nicholls in *N.Q. Nat.*, Sept. and Dec., 1938. Syn. *Bulbophyllum lichenastrum* F. Muell. *Fragm.*, l.c.; Bail. *Q. Fl.* 1537. Mueller had apparently placed this diminutive plant first in *Dendrobium*, but he described it as a *Bulbophyllum*. Kranzlin places it in *Dendrobium*. Following is a free translation of his remarks: "As Ferd. Mueller rightly suspected, it is more satisfactory to ascribe this little plant to Dendrobium. The form of the labellum is perhaps, after a fashion, similar to that of Bulbophyllum, nevertheless it is not the same. Except for the labellum, all the characters indicate the section Strongyle" (i.e., in *Dendrobium*). Nicholls was apparently not aware of Kranzlin's treatment of the plant when he transferred it to *Dendrobium* in *N.Q. Nat.*, l.c. His figures of the floral details show close affinity with his own *D. aurantiaco-purpureum*, but the leaves are very different. There can be no doubt, as Nicholls states, that Fitzgerald misinterpreted Mueller's *Bulbophyllum lichenastrum*. The specific name is remarkably apt, and a patch of this tiny plant growing on a rock might easily be mistaken for a lichen or a liverwort. On the other hand, there is no such resemblance in the plant depicted by Fitzgerald. *D. lichenastrum* is probably the smallest known species of the genus. The creeping rhizomes form dense patches on trees or rocks, and are concealed by the very numerous, thick leaves, barely 1 cm. in length, and often as broad as long. The diminutive solitary flower, on a relatively long pedicel, is whitish with branching red lines, and an orange labellum. The species is not uncommon about the Bellenden Ker Range and the Atherton Tableland in North Queensland. (Text-fig. 3, B.)

40. D. LINGUIFORME Sw. in *K. Akad. Stockh. N. Handl.* (1800), 247; *Sm. Ex. Bot.* I (1804), t. 11; Rupp, illustr. in *Guide to Orch. N.S.W.* (1930), 31. This was the first Australian Dendrobe to be described. The author, Swartz, was also the founder of the genus. *D. linguiforme* was named from its thick, tongue-like leaves. It creeps, often in large masses, on rocks or trees, and is common in many districts of eastern

Australia from southern N.S.W. to tropical Queensland. The short racemes of densely set white flowers are very attractive. A yellow-flowering form has been recorded in northern N.S.W. (Fordham, at Brunswick Heads), but has not been named.

Var. *Nugentii* Bail. *Q. Fl.* 1533. A north Queensland form with almost rotund leaves and smaller flowers.

Var. *Huntianum* Rupp in *A.O.R.* Sept., 1942, 40. A form from the Upper Brisbane River, Queensland, blooming two to three months earlier than the type form. Leaves often very long; inflorescence approaching that of var. *Nugentii.* In continued cultivation this variety shows a tendency to revert to the type form.

41. D. LUTEOCILIUM Rupp in *N.Q. Nat.*, Dec., 1945. This species was discovered at Babinda, North Queensland, by J. H. Wilkie in October, 1945. It seems to be closely related to several New Guinea species described by Schlechter in Fedde, Rep. i (1914), 573–618, but is sufficiently distinct for specific rank. A rather tall plant with leafy, somewhat flattened stems. Flowers a little more than 2 cm. in diameter, in pairs, yellowish-green, very fugacious. Labellum with a conspicuous patch of yellow cilia near the apex of the mid-lobe. (Text-fig. 4.)

42. D. MORTII F. Muell. *Fragm.* i (1858), 214; Rupp in *Q. Nat.*, August, 1934, 51, et in *A.O.R.*, Sept., 1941, 57. Syn. *D. Bowmanii* Benth. 286. Bailey correctly describes this species in *Q. Fl.* 1534, but then strangely proceeds to a description of Bentham's *D. Bowmanii*, which he distinguishes from it. Bentham most evidently mixed up Mueller's specimens of *D. Beckleri* and *D. Mortii*; he suppressed the former, but described it as *D. Mortii*, and then established a new species, *D. Bowmanii*, from north Queensland specimens of *D. Mortii*. There is no appreciable difference between the northern and southern forms of this species. The leaves of the former are a trifle more robust, and the labellum is more obtuse. *D. Mortii* is one of the so-called "Pencil Orchids", allied to, but quite distinct from, *D. Beckleri* and *D. striolatum*. An interesting characteristic is its production of several "crops" of flowers in succession, from late January to April or May. It extends from about the Clarence River in N.S.W. northward into the Queensland tropics.

43. D. OPHIOGLOSSUM Rchb. f. in *Journ. Linn. Soc. London*, xv (1877), 113; Krzl., *Pflanz.* 135; C. T. White in *A.O.R.*, June, 1943, 19. It is difficult to give any satisfactory account of this species. It has been known only from a solitary specimen in Kew Herbarium, collected at Cape York in 1874 by H. N. Mosely of the "Challenger" Expedition. It was described by H. G. Reichenbach from this specimen. Kranzlin, l.c., stated that the specimen was in very bad condition; but he disagreed with Rolfe, who had expressed the opinion that it was identical with *D. Smilliae.* In *A.O.R.*, l.c., White published an article (illustrated by a very fine photograph) under the heading "Has *D. ophioglossum* been re-discovered?". The re-discovery, however, if such it be, is not in Australia, but in the Solomon Islands. A plant from there was successfully grown by C. A. Dunn in Brisbane. White admits certain differences in the floral details of this plant from those described by Reichenbach and Kranzlin; but it seems to us that these are such as might be accounted for by the difference between a damaged and long-dried specimen and a living flower. We think that White makes out a good case for the identity of the Solomon Islands plant. If he has interpreted it correctly, there can be no doubt that *D. ophioglossum* and *D. Smilliae* are distinct species. Habit and inflorescence are similar, but the individual flowers are quite different. The Solomon Island flowers appear to us to be nearer to those of the New Guinea *D. bracteosum.* It is to be hoped that *D. ophioglossum* will be found again in its type locality. Dr. H. E. Young, who contributes an article on the orchids of Cape York in *A.O.R.*, March, 1947, apparently saw no plant there which could be interpreted as this species.

44. D. PHALAENOPSIS Fitzg. This has been dealt with above under *D. bigibbum.*

45. D. PRENTICEI (F. Muell.) Nicholls in *N.Q. Nat.*, Sept. and Dec., 1938. Syn. *Bulbophyllum Prenticei* F. Muell. in *Wing's S. Sci. Rec.*, 1881, 173. This is another of the

diminutive North Queensland orchids which Nicholls, l.c., places in *Dendrobium*. In allusion to this species he remarks, "It is difficult to assign this plant satisfactorily to either *Bulbophyllum* or *Dendrobium*", and then suggests that the absence of a pseudobulb should exclude it from the former genus; but we have already pointed out in connection with *D. aurantiaco-purpureum* that this argument is not sound. It might be urged with equal force that the lobeless labellum should exclude it from *Dendrobium*; but we cannot bind plants to hard-and-fast rules, and as there are species of *Bulbophyllum* without pseudobulbs, so there are species of *Dendrobium* with entire labella. For ourselves, we endorse Nicholls's transfer of this plant mainly on the ground of its very obvious close affinity with *D. aurantiaco-purpureum*, *D. lichenastrum*, and *D. variabile*. If, as we believe, these three are rightly assigned to *Dendrobium*, it would be absurd to place *D. Prenticei* in a different genus. Indeed, we do not feel sure that *D. aurantiaco-purpureum*, which appears to be the rarest of the plants in this group, might not with advantage be considered a sturdy variety of *D. Prenticei*. The morphological distinctions do not seem to be great. (Text-fig. 3, D.)

46. D. SCHNEIDERAE Bail. in *2nd Suppl. Synopsis Q. Fl.* (1888), 57, et *Q. Fl.* 1531. This small species, which is found in southern Queensland and northern N.S.W., might be mistaken for a depauperate form of *D. monophyllum*, but the pseudobulbs are smaller and the leaves are more often paired than solitary. The racemes are weak and drooping, with a few small yellowish flowers. The only known variety is a far more attractive orchid than the type form.

   Var. *major* Rupp in *Q. Nat.*, Jan., 1939. Discovered in the Eungella Range, Mackay district, Queensland, by Dr. C. P. Ledward in 1937. Larger than the type form; racemes strong and erect, but gradually curving, up to 18 cm. long; flowers similar to those of the type, but from 12 to 25.

47. D. SMILLIAE F. Muell. *Fragm.* vi (1867), 94; Rchb. f. in *Gard. Chron.* (1886), II, 552; Benth. 282; Bail. *Q. Fl.* 1530. Syn. *Coelandria Smilliae* Fitz. *A.O.* 1, 7. Fitzgerald thought this so unlike any species of *Dendrobium* with which he was acquainted that he established a new genus to accommodate it. His action, however, has not been endorsed. Quite a number of *Dendrobium* species share its peculiar form of inflorescence. It is closely related to *D. Hollrungii*, and in our note on that species we have suggested that Rendle's *D. Hollrungii* var. *australiense* might be transferred to the present species. *D. Smilliae* is a robust species up to 90 cm. high. The flowers are borne in small, densely-packed racemes; individually they are not large, but the racemes are often borne in great profusion. Reichenbach, l.c., gives a glowing description of the beauty of this orchid. The flowers are red, tipped with green. The individual flower is tubular above the spur, and the perianth segments are free only towards their apices. Capsules waxy-white. The species is not uncommon in North Queensland.

48. D. SPECIOSUM Sm. *Ex. Bot.* I (1804), 17, t. 10; Benth. 279; Bail. *Q. Fl.* 1526; Fitzg. *A.O.* ii, 4; *Bot. Mag.* 3704; *Orch. N.S.W.* 113; *A.O.R.* March, 1937, 7, et Sept., 1946, 65. Bentham remarks on the misrepresentation of the flowers in Sir J. E. Smith's plate; and indeed they are almost unrecognizable. Although this fine species, ranging from eastern Victoria northward into the Queensland tropics, is familiar to many people under the inappropriate vernacular name of "Rock Lily", it presents great difficulties to those who wish to see distinguishing names attached to its numerous varieties. Botanists have attempted to meet this demand, but with indifferent success, the variations being so often inconstant. Three forms which were originally described as varieties of *D. speciosum* are now recognized as species, viz., *D. fusiforme*, *D. delicatum* and *D. gracillimum*. On the other hand, Hooker's *D. Hillii* is now only ranked as a variety of *D. speciosum* with tall stems and smaller individual flowers. Bailey, l.c., records three varieties—*Hillii, curvicaule* and *nitidum*—and two "forms" of var. *Hillii—Bancroftianum* and *grandiflorum*. Kranzlin (*Pflanz.* 271) identifies forma *Bancroftianum* with *D. delicatum*; but we cannot endorse this, as *Bancrof-*

tianum is described by H. G. Reichenbach as a plant with the robust habit of *D. speciosum*, the floral segments longer and narrower. Why Bailey placed his form *grandiflorum* under var. *Hillii* and not under the species itself is not clear. We have not seen his var. *curvicaule*; but from the description he gives, it would appear to merit more than varietal rank. His var. *nitidum* has been discussed in connection with *D. gracillimum* above, as it may prove to be the white-flowering form of that plant; but no specimens are known at present.

49. D. SUPERBIENS Rchb. f. in *Gard. Chron.* (1876), II, 516, et ibid. (1878), I, 40; Krzl., *Pflanz.* 258; Fitzg. *A.O.*, ii, 1; *A.O.R.* Dec., 1939, 111. This well-named species is considered by some botanists and growers to be of hybrid origin, *D. bigibbum* var. *Phalaenopsis* × *D. undulatum*. Bailey, in *Q. Fl.* 1524, distinguishes between it and Mueller's *D. Fitzgeraldii*, which he considers to be the subject of Fitzgerald's plate; but it is generally conceded that the two are synonymous. *D. superbiens* exhibits considerable variation in shades of colour between purple and red, and in some forms the segments of the flowers are more undulate, or even twisted, than in others. H. G. Reichenbach's *D. Goldiei* (see excluded species above) is a form of *D. superbiens* with deep purplish-red flowers and very slight undulation in the floral segments. Fitzgerald's splendid plate is an admirable representation of this very beautiful species as it is most commonly known to growers. We do not know of any definite record of its occurrence on the mainland of Australia, but it is found on the adjacent islands of Torres Strait. In Dr. H. E. Young's article on the orchids of Cape York already referred to (*A.O.R.* March, 1947), he does not mention seeing it on the Peninsula, though both of its putative parents were abundant there; but he found it on Prince of Wales Island.

50. D. TENUISSIMUM Rupp in these PROCEEDINGS, lii (1927), 570, et in *Q. Nat.*, August, 1934, 52. This dainty species is closely allied to *D. Mortii* and *D. Beckleri*, but could not be included in either. It was described from specimens found on the Upper Allyn River, in the southern foothills of Barrington Tops, N.S.W., but has been found since then in other localities, northward to the mountains of southern Queensland. It is discussed here chiefly to call attention to the fact—recorded in *Q. Nat.*, l.c.— that Mueller recognized it as a distinct species as far back as 1883, but never published it. This was not known to Rupp until seven years after he had described it.

51. D. TERETIFOLIUM R. Br. 333; Benth. 285; *Bot. Mag.* 4711; Bail. *Q. Fl.* 1533; Rupp in these PROCEEDINGS, lx (1935), 155; *A.O.R.*, June, 1943, 34. This species was discussed and reviewed at some length in these PROCEEDINGS, l.c., where a third variety was added to the two recorded by Bailey in *Q. Fl.* The type form, with white or pale cream flowers, is common in N.S.W. from the south coast northward to Byron Bay. There for the first time appears the yellow-flowering var. *aureum*, which becomes the dominant form in southern Queensland. Further north it disappears again and the north Queensland var. *fasciculatum* has white flowers, but in a strikingly different inflorescence. Var. *Fairfaxii*, for which Bailey seems to have mistaken this northern form, is now regarded in N.S.W. as the rain forest form of the species. Intermediates between it and the type form may often be found where rain forest meets open forest, but the latter is very rarely seen inside the rain forest. All the forms of *D. teretifolium* tend to produce giant and dwarf flowers. This habit, of course, is found in many other orchids, but it is certainly very characteristic of the present species. Even on the same tree, one plant may have flowers twice as large as those of its neighbours. Although the individual flower is furnished with very attenuated segments, the profusion of the racemes makes *D. teretifolium* a most attractive species when in full bloom, and has earned for it in some districts the rather appropriate vernacular name of "Clematis Orchid". One of us remembers a swamp-oak on the Myall Lakes in N.S.W. which in August could be clearly identified from the hills four miles away, by the masses of snowy blooms hanging from trunk and branches. He estimated that the tree carried at least 100 plants.

52. D. TETRAGONUM Cunn. in Lindl., *Bot. Reg.* (1839), Misc. 33; Benth. 279; *Bot. Mag.* 5956; Bail. *Q. Fl.,* 1527; *Orch. N.S.W.* 117; Gilbert in *A.O.R.* Dec., 1937, 19, et ibid. June, 1942, 36; Nicholls in *A.O.R.* Sept., 1942, frontispiece and p. 40. This is the only Australian *Dendrobium* with quadrangular stems, and is therefore easily identified by this peculiar character. Like so many other species, it is very variable. Four varieties have been named, three by Gilbert, *A.O.R.,* l.c., and one by Nicholls in the same journal. The range of the species from south to north is much the same as that of *D. teretifolium,* but it does not extend so far from the coast as the latter. Like that species, it produces giant and dwarf flowers; but in each of the known forms, allowing for a slight margin either way, the floral dimensions remain constant. The type form has the smallest flowers; this is the common N.S.W. form. Gilbert's var. *Hayesianum* was discovered in the Illawarra district south of Sydney, but though comparatively rare, it is now known to have the range of the species. It is in Queensland, particularly in the north, that the giant flowers are most in evidence. Expanded sepals of var. *giganteum* have been measured 28 cm. from tip to tip. These large flowers are also more richly coloured than the small ones. Often they bear a striking (but superficial) resemblance to those of the terrestrial *Caladenia Patersonii,* and like the latter, the species is sometimes called "Spider Orchid". Nicholls's var. *tomentosum* is one of these northern "Spiders", its varietal name alluding to the unusual tomentose labellum. The plate in *Bot. Mag.,* l.c., shows flowers somewhat similar to those of var. *Hayesianum,* but more robust. A form with small cream flowers is reported from Proserpine, North Queensland; but we have not seen this, and the report has come too late to enable us to give any definite information here.

53. D. UNDULATUM R. Br. 332; Lindl. *Gen. and Sp. Orch.* 87; Benth. 279; Fitzg. *A.O.* ii, 3; T. T. Taylor in *A.O.R.* June, 1944. Syn. *D. discolor* Lindl. *Bot. Reg.* 1841, t. 52.

This is the "Golden Orchid" of Queensland; and we cordially commend Taylor's article just cited as an admirable account of one of the largest and most spectacular plants in the whole range of *Dendrobium* species. Those of us who know *D. undulatum* only from occasional specimens seen in orchid exhibitions or private collections can form little idea of the magnificence of this regal plant in its native habitat, so ably described by Taylor. It is not easily cultivated outside the tropics unless assisted by artificial heat; yet in its native haunts it is exceedingly hardy, braving the elements on wind-swept mountains, or often clinging to bare rocks where it is splashed by the salt spray of wild seas. Sometimes it exceeds 5 m. in height. The flowers, borne profusely on large racemes, are a rich golden brown or bronze colour. The plant exhibits a marked tendency to produce "multiple" flowers, sometimes with their segments joined back to back, or sometimes with 8 to 10 undersized flowers massed together on one pedicel, forming a miniature raceme within a raceme. The species is found northward from Port Curtis to Cape York, and is abundant on many of the islands off the Queensland coast. It extends to New Guinea and the Solomon Islands. The specific name is of course in allusion to the characteristic undulation of the perianth segments.

Var. *fimbrilabium* Rchb. f. in *Gard. Chron.* (1878), I, 40. Lateral lobes of the labellum fimbriate.

Var. *Broomfieldii* Fitzg. *A.O.* ii, 3 (double-page plate). Stems rather angular; flowers bright canary-yellow.

54. D. VARIABILE Nicholls in *N.Q. Nat.* Sept. and Dec., 1938. We confess that we find considerable difficulty in reaching any satisfactory conclusion about the identity of this diminutive species. The author directs attention to an error in the key accompanying his plate, where *D. variabile* is named *D. dimorphum.* It is figured along with *D. lichenastrum* and *D. Prenticei.* The close relation between the latter and *D. variabile* is evident, *D. Prenticei* showing less variation in the form of the leaves, and bearing a shorter pedicel for the flower. But with living plants, of which we have both received specimens from the Atherton Tableland and other

Text-fig. 4.—*Dendrobium luteocilium.*　Inset: Upper surface of labellum (enlarged).
Text-fig. 5.—*Dendrobium Wilkianum.*　Inset: Upper surface of labellum (enlarged).

North Queensland areas, we do not find it so easy to distinguish between the species as Nicholls's plate would suggest. We recognize that this group of small orchids, which includes *D. aurantiaco-purpureum* also, presents a very formidable problem in taxonomy; and it is with full appreciation of the value of his efforts to solve that problem, that we again express the hope that Nicholls will yet give us a more complete exposition of the solution he considers he has reached. (Text-fig. 3, C.)

55. D. WILKIANUM Rupp in *N.Q. Nat.*, Dec., 1941, and March, 1942. This species was discovered by G. Bates and Kerns in the Cairns district of North Queensland in 1934; but was not described until J. H. Wilkie sent a living plant from the same area (Babinda) in 1941. It is a robust plant, in habit somewhat resembling a gigantic *D. aemulum*, but the flowers are very different. They are comparable in size with those of *D. undulatum* or *D. fuscum*, and the affinities of the species appear to be chiefly with the latter; but there is neither undulation nor twisting in the perianth segments. Racemes carry from 3 to 12 flowers of a dull brownish colour, the labellum being yellowish-green, traversed by numerous dark red lines across the lateral lobes. (Text-fig. 5.)

Doubtful Species.

D. QUADRILOBUM Rolfe in *Kew Bull.*, 1896, 44; Rupp in *N.Q. Nat.*, March, 1942. Late in 1941 Rupp received from the Brisbane Herbarium a small specimen consisting of a few pseudobulbs, one mutilated leaf, and two perfect flowers. It was obviously a *Dendrobium*, and was collected by K. Kennedy 20 miles west of Paluma, which is about 60 miles from Townsville, North Queensland. It was very distinct from any known Australian species, and Rupp proposed to describe it under the name *D. quadrilobum*, in allusion to the conspicuously bifid mid-lobe of the labellum, which gave that segment the appearance of being 4-lobed. Discovering, however, that this name had been already used by Rolfe, he studied the description given by

Rolfe in *Kew Bull.*, l.c. The name was applied to a plant received from Australia, but no locality was given; and Rolfe expressed the view that it came from New Guinea or one of the adjacent islands. The description of the flowers seemed to fit Kennedy's plant pretty well. But Rolfe assigned his species to the section *Cadetia*, which has since then been removed from *Dendrobium* and restored to generic rank. It would be quite out of the question to place the Paluma plant in *Cadetia*. It is a genuine species of *Dendrobium*, and in Rupp's opinion belongs to the section *Cuthbertsonia*. The flowers are large in proportion to the plant; the longest pseudo-bulb of the plant in Rupp's collection at the Sydney Herbarium measures 3 cm., and the flowers are 2 cm. in diameter. We cannot be sure, then, whether this plant is really Rolfe's *D. quadrilobum* or an undescribed species. Unfortunately the specimens which Kennedy had in cultivation were destroyed by rats, and he has been unable to find any more plants which can be definitely identified with those of 1941. He has sent down one obtained about five miles from the original locality, but this appears to us to be a very young plant of *D. fusiforme*; at all events, it is unlike the 1941 specimens. For the present, therefore, the identity of the Paluma species is doubtful; but since it was unquestionably found growing in Australia, and cannot be included in any known Australian species, we think it right to record it here.

In the above review we have not attempted to provide detailed re-descriptions of the Australian species of *Dendrobium*, but with few exceptions have confined ourselves to indicating the salient points of distinction. On the whole, our paper may be regarded as an expansion and revision of White's synopsis in *A.O.R.*, loc. cit. We hope that it may serve as a stepping-stone towards some future exhaustive monograph on the Australian Dendrobiinae. The author of any such work may find it helpful to be spared the necessity of investigating the excluded species of *Dendrobium* which we have enumerated; and to have available in one publication the notes and references provided above. The time is not yet ripe for such a monograph. Not only is it likely that new species of *Dendrobium* still await discovery; but considerable additions will almost certainly be made to the number of Australian species of the allied genus *Bulbophyllum*, which, although placed by Pfitzer in a separate tribe, approaches very closely to *Dendrobium* in Australia, and might well be dealt with in the same publication.

In conclusion, we desire to express our thanks to all those who, either by sending specimens or answering inquiries or offering suggestions, have made this review possible. It has involved upward of seven months of investigation, and without the help of our many friends we could not have carried it out. We must also acknowledge our great indebtedness to the libraries of the National Herbaria in Sydney and Brisbane, where we have had access to nearly all the publications to which we have made reference.

LARVAL SMARIDIDAE (ACARINA) FROM AUSTRALIA AND NEW GUINEA.

By R. V. SOUTHCOTT, M.B., B.S., D.T.M. & H. (Sydney).

(Eight Text-figures.)

[Read 24th September, 1947.]

The first larval mite proven to belong to the family Smarididae Kramer 1878 was that of *Smaris prominens* (Banks, 1916), a species widely distributed in Australia. It was referred to this family by Womersley and Southcott in 1941, following experimental rearing of larvae taken in the field, parasitic upon the Psocopteron *Troctes divinatorius* L., to nymphs, which were easily correlated with adults taken in the same locality.

The genus *Hauptmannia* was erected by Oudemans in 1910 for his *Achorolophus longicollis*, a larval prostigmatid mite from Friesland, in Holland, described earlier in the same year. A second species, *H. brevicollis* Ouds. 1910, from Holland, was also referred to the genus. No further species were referred to the genus until 1934, when Womersley briefly described two species from Western Australia. *Hauptmannia* was referred to the family Erythraeidae by both Oudemans and Womersley. In 1946 Southcott pointed out that all larvae proven as Erythraeidae had the two lateral claws of the tarsi of the legs dissimilar, whereas in *Smaris* the lateral claws are identical, heavily ciliated, and that in *Hauptmannia* the lateral claws are identical, though unciliated. This similarity in arrangement between larval *Smaris* and *Hauptmannia*, plus the difficulty in fitting *Hauptmannia* into a scheme of larval Erythraeidae that was the result of a considerable amount of experimental rearing, caused the writer to suggest that *Hauptmannia* should be referred to the Smarididae, and on grounds of its geographical distribution, was possibly the larva of *Hirstiosoma* Womersley 1934.

In this paper Womersley's two Western Australian species—*Hauptmannia westraliensis* and *H. mullewaensis*—are re-described. A further species, *H. aitapensis* n. sp., from New Guinea, which is quite close to the genotype, is also described.

An aberrant larval prostigmatid mite from New Guinea, *Clipeosoma copiolarum* n. gen., n. sp., is described in this paper. It is referred to the Smarididae rather than to the Erythraeidae on account of its having identical lateral tarsal claws, these being ciliated, but so heavily so as in *Smaris*.

In this paper all the known larvae of the Smarididae are keyed, and an attempt is made to evaluate the characters of the larval genera.

Key to the Larval Genera referred to the Family Smarididae.

A.   Eyes two on each side.
Dorsal scutum broader than long, roughly triangular or crescentic. Lateral tarsal claws identical, heavily ciliated, pulvilliform .... *Smaris* Latr. 1796
Known from only *Smaris prominens* Bks. 1916 (Australian).

AA.   Eyes one on each side.
B.   Anterior sensilla of dorsal scutum are anterior to the anterior pair of non-sensillary scutal setae. Claws of tarsus of leg ciliated. Palpal claw trifurcate, the third claw being short, basal, lying ventrally. Mandibles slender .... *Clipeosoma*, n. gen.
Genotype *Clipeosoma copiolarum*, n. sp. (New Guinea).

BB.   Anterior sensilla of dorsal scutum are behind the anterior pair of non-sensillary scutal setae. Claws of tarsus of leg not ciliated. Palpal claw single or bifurcate; the palpal tibia also carries a stout accessory peg or claw. Mandibles compact .... *Hauptmannia* Ouds. 1910.
Genotype *Achorolophus longicollis* Ouds. 1910.
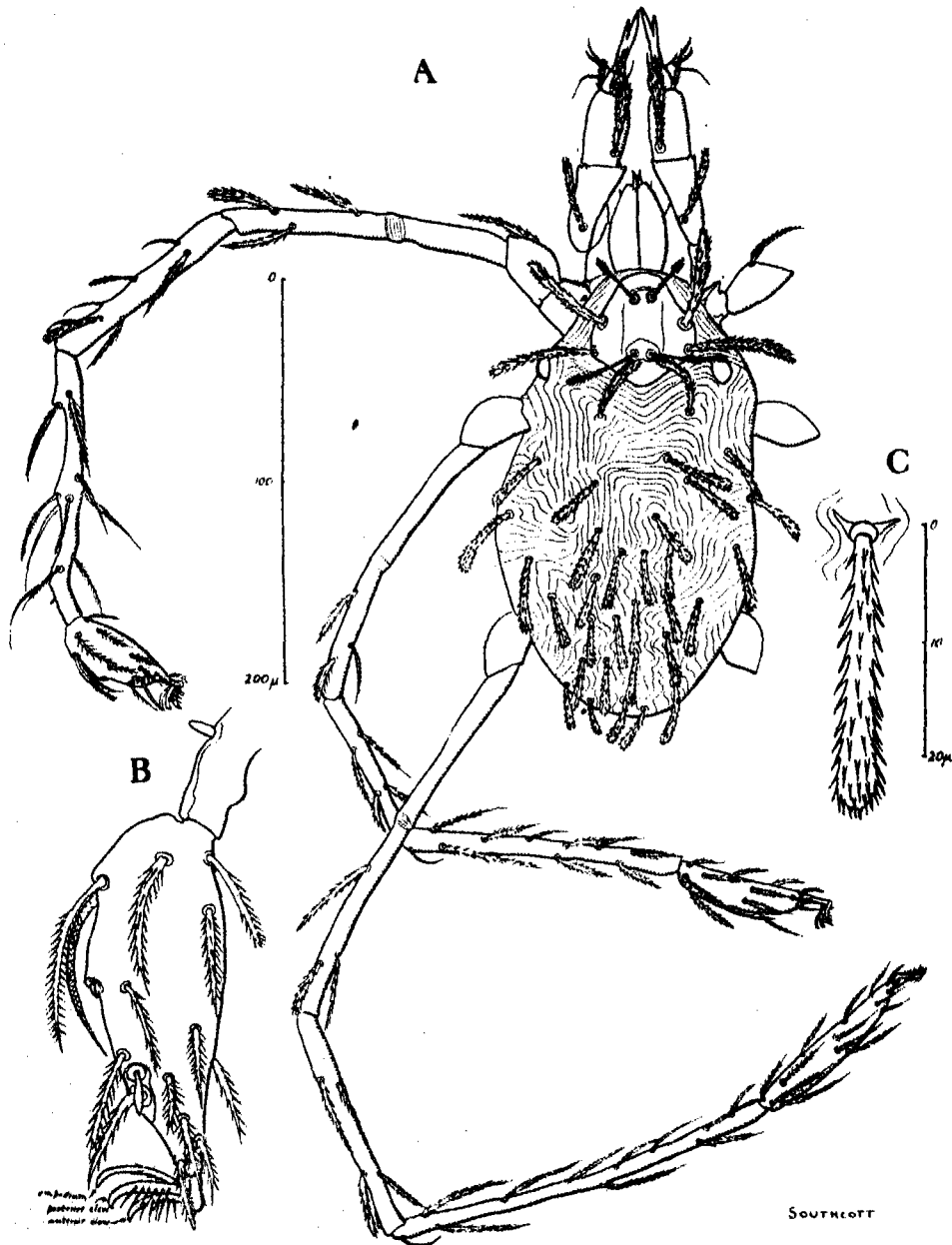
Fig. 1.—*Clipeosoma copiolarum*, n. gen., n. sp. Larva. A, Dorsal view; B, Tarsus I, posterior aspect; C, Dorsal seta.

Genus SMARIS Latreille.

Précis car. gén. Ins., 1796, 180.

Definition of Larval Characters.—Eyes two on each side. Dorsal scutum broader than long, roughly triangular or crescentic, with two pairs of sensillary setae and two pairs of non-sensillary setae. The anterior pair of scutal sensillary setae arises between the levels of the anterior and posterior pairs of scutal non-sensillary setae; the posterior pair of sensillary setae arises at the posterior edge of the scutum. Ventrally one pair of setae between coxae I; one pair of setae between coxae III. Each coxa with one seta.

Each tarsus with one seta. Each trochanter with one seta. Tarsus I with a Haller's type organ, not present on tarsus II or III; tarsus I and II, but not III, with a solenoidal spine. Lateral tarsal claws identical, heavily ciliated, pulvilliform. Mandibles compact, rounded posteriorly.

Remarks: The above definition is based on one species only, *S. prominens* (Banks 1916), Australian, described by Womersley and Southcott (1941).

Corrigendum: In the figure of the larva of *Smaris prominens* given by Womersley and Southcott, 1941 [*Trans. Roy. Soc. S.A.*, 65 (1)], page 66, Fig. 2B, the trochanter of leg I appears to have two setae. Actually the proximal seta shown belongs to the coxa, and the distal seta only belongs to the trochanter; thus both coxa and trochanter of each leg have only one seta each.

Genus CLIPEOSOMA, n. gen.

Definition: Eyes one on each side. Dorsal scutum trapezoidal, with two pairs of sensillary setae and two pairs of non-sensillary setae. The anterior pair of sensillary setae arises anterior to the anterior pair of non-sensillary scutal setae; the posterior pair of sensillae arises well anterior to the posterior angle of the shield. Ventrally one pair of setae between coxae I, a further pair of setae between the levels of coxae II and III. Each coxa with one seta. Each trochanter with one seta. Tarsus I with a Haller's type sensory organ; not present on II or III. Tarsus I and tarsus II, but not III, carry a solenoidal spine. Lateral tarsal claws identical, falciform, ciliated. Mandibles slender. Claw of palpal tibia trifurcate, the third claw short, basal, lying ventrally.

Genotype: *Clipeosoma copiolarum*, n. sp.

CLIPEOSOMA COPIOLARUM, n. sp. Fig. 1, A–C; Fig. 2, A, B.

Description of Larva (Type): Colour red. Body an elongate ovoid, 210μ long by 110μ wide. Dorsal scutum trapezoidal, with rounded angles, length 54μ, width 52μ. Scutum with two pairs of heavily ciliated slightly clavate sensillary setae, anterior 26μ long, posterior 40μ long; scutum also with 2 pairs of non-sensillary setae, stout, clavate and heavily ciliated, anterior 49μ long, posterior 52μ long. The anterior sensillary setae arise well anterior to the anterior pair of non-sensillary setae. Distance between centres of anterior and posterior sensilla 26μ. Posterior sensilla arise well in advance of the posterior angle of the shield, and slightly behind the level of the posterior pair of non-sensillary scutal setae. Anterolateral borders of shield slightly concave, posterolateral borders also slightly concave. Eyes one on each side, level with the posterior end of the shield. Dorsum with about 31 setae, brown, stout, clavate, with dagger-shaped ciliations, setae 22–38μ long, arranged in irregular rows across the dorsum. Venter: between coxae I a pair of long, pointed, heavily ciliated setae, 39μ long; between the levels of coxae II and III a similar pair, 39μ long; behind coxae III are 6 setae, heavily ciliated, the first row is of 4 setae, pointed apically, 20–23μ long; the second row is of 2 setae, blunted, 16μ long. Each coxa with one seta: that on I long, pointed, ciliated, 49μ long; on II similar, 33μ long; on III blunted, heavily ciliated, 27μ long. Legs long and thin: I 505μ long, II 520μ, III 655μ (all lengths including coxae and claws). Each trochanter with one seta. Tarsus I relatively thickened, 55μ long by 24μ high ((exclusive of claws and columella). Tarsus I with a Haller's type sensory organ, not present on II or III; tarsus I and II, but not III, with a solenoidal spine. Tarsal claws strong, falciform, with ventral ciliations; empodium falciform, slender, with dorsal and ventral ciliations. Metatarsus I sinuous, irregular, 133μ long, provided with various sensory setae. Capitulum: mandibles slender; chelicerae slender, with a short, straight cutting edge, without teeth or spurs. Palpi strong, elongate. Palpal coxa, femur, genu, tibia, tarsus with 0, 1, 1, 3, 6 setae respectively. Claw to palpal tibia trifurcate, dorsally there is a long medial and shorter lateral claw, ventrally there is a short conical basal claw (Fig. 2, B). Palpal tarsus as figured.

Locality: Babiang, in the Aitape region of New Guinea, a single specimen (Type), on the floor of the rain-forest, 19th December, 1944 (R.V.S.).

Type in author's collection (ACA 1889).
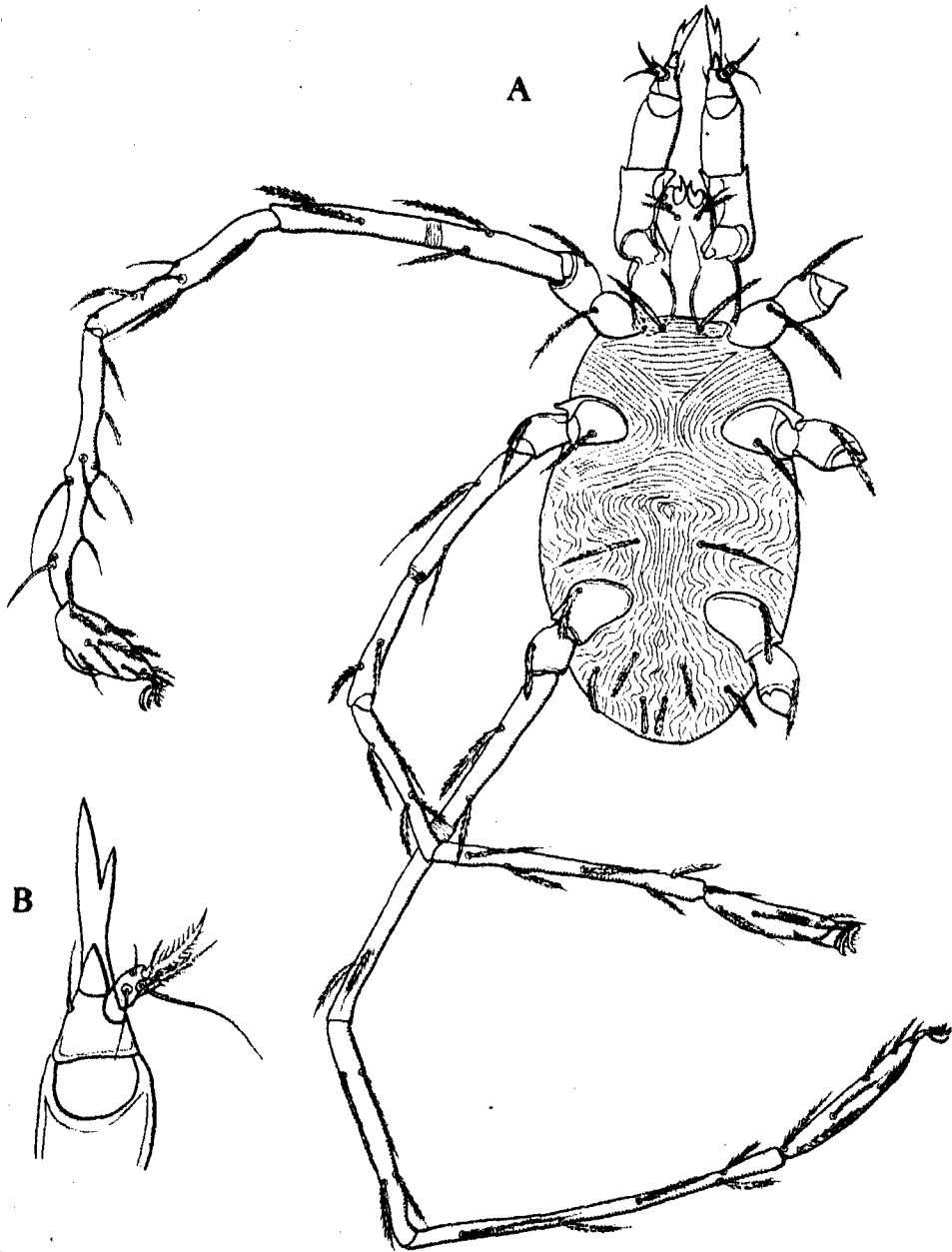
Fig. 2.—*Clipeosoma copiolarum*, n. gen., n. sp. Larva. A, Ventral view; B, Tip of palp, ventral view.

Genus HAUPTMANNIA Oudemans 1910.

Ent. Bericht., 1910, 3 (52): 48.

Genotype: Achorolophus longicollis Ouds. 1910.

Re-definition of Genus: Eyes one on each side. Dorsal scutum fairly broad, of varying shapes; with 2 pairs of sensillary setae and 2 pairs of non-sensillary setae; the anterior pair of sensillary setae lying between the levels of the 2 pairs of non-sensillary setae. Ventrally there are a number of setae between and behind coxae I, and between

the levels of coxae II and III. Coxa I with one seta, coxae II and III with one or 2 setae each. Each trochanter with 2 setae (in all the Australasian forms; possibly with only 1 seta in the European forms). Lateral tarsal claws identical, falciform, unciliated. Palpal femur with 2 setae. Palpal tibia with a strong simple or bifurcate claw, and also with a stout accessory peg or claw. Mandibles compact.

Key to the Larval Genus Hauptmannia

A. Claw of palpal tibia simple. Basis capituli with one seta on each side posterior to the palpal coxae. Posterior sensillary setae of dorsal scutum arise on the posterior edge of the scutum.
    B. Palpal tarsus with a pectinate seta.
        C. Setae between coxae I much longer than the setae on coxae I ....
        .... *H. longicollis* (Ouds. 1910) (European)
        CC. Setae between coxae I equal in length to, or shorter than, setae on coxae I
        .... *H. aitapensis*, n. sp. (New Guinea)
    BB. No pectinate seta on palpal tarsus .... *H. brevicollis* Ouds. 1910 (European)
AA. Claw of palpal tibia bifurcate. No setae on basis capituli behind palpal coxae. Posterior sensillary setae of dorsal scutum arise well anterior to the posterior edge of the scutum.
        D. Each coxa with one seta. Posterior sensillary setae of the dorsal scutum arise posterior to the middle of the shield. Dorsal scutum roughly oblong, with rounded corners, porose, without striations ....
        .... *H. westraliensis* Wom. 1934 (West Australian)
        DD. Coxa I with one seta, coxae II and III each with 2 setae. Posterior sensillary setae of dorsal scutum arise anterior to the middle of the shield. Shield heart-shaped, with a conspicuous waist, porose and also with striations ....
        .... *H. mullewaensis* Wom. 1934 (West Australian)

HAUPTMANNIA AITAPENSIS, n. sp. Fig. 3, A–F; Fig. 4.

Description of Larva (*Type*): Colour red. Body ovoid, 350μ long by 220μ wide. Dorsal scutum pentagonal, 53μ long by 41μ across; the anterior margin of the shield slightly concave, the anterior part of the lateral margins straight, and parallel with each other, the posterior part of the lateral margins straight, and running obliquely medially and posteriorly to the blunt rounded posterior angle of the shield. Scutum with 2 pairs of fine, pointed, faintly ciliated sensillary setae; anterior pair 24μ long, posterior 56μ; with 2 pairs of non-sensillary setae, tapering, pointed, with fine adpressed ciliations, anterior 41μ long with bases 35μ apart, posterior 30μ long with bases 35μ apart, distance between centres of anterior and posterior sensilla 41μ. The anterior sensillary setae arise a little behind the level of the anterior non-sensillary setae, posterior sensillary setae arise at the posterior angle of the shield. Eyes one on each side, lateral to the posterolateral margins of the shield. Dorsum with about 47 tapering, pointed, curved setae, lightly pigmented, 20–31μ long, with fine ciliations. Dorsal setae arranged 2, 2, 2, 4, 8, 7, 6, 4, 6, 4, 2. Venter: between coxae I a pair of curved spiniform setae, with very faint adpressed ciliations, 31μ long; between coxae I and II are 4 similar setae, but with the ciliations a little more marked, 24–30μ long; between coxae II and III a number of similar faintly ciliated setae, and also behind coxae III, 14–26μ long. The more posterior setae are the stronger, and have freer ciliations. Each coxa with one seta, pointed, tapering, with fine ciliations; on 1 31μ long, on II 18μ, on III 20μ. Legs fairly stout, I 300μ long, II 275μ, III 315μ (all lengths including coxae and claws). Each trochanter with 2 setae. Tarsi short, swollen. Tarsus I 41μ long by 24μ high (exclusive of claws and columella); dorsal setae of tarsus unciliated, ventral setae ciliated; solenoidal spine present on the dorsum of tarsus I and II, not on III. Tarsal claws strong, falciform, unciliated, identical, ridged obliquely along their sides; empodium slender, falciform, simple. Metatarsi stout, clavate; metatarsus I 52μ long. Capitulum: mandibles compact; chelicerae stout, falciform, simple. Palpi strong, short; palpal coxa, femur, genu, tibia, tarsus with 0, 2, 3, 2, 8 setae respectively. Claw of palpal tibia single, bent over at the tip, and there excavated a little on the ventral side; the palpal tibia also carries an accessory claw on its dorsomedial aspect, close to the main palpal claw, with, however, a distinct separation. Palpal tarsus with various (8) sensory
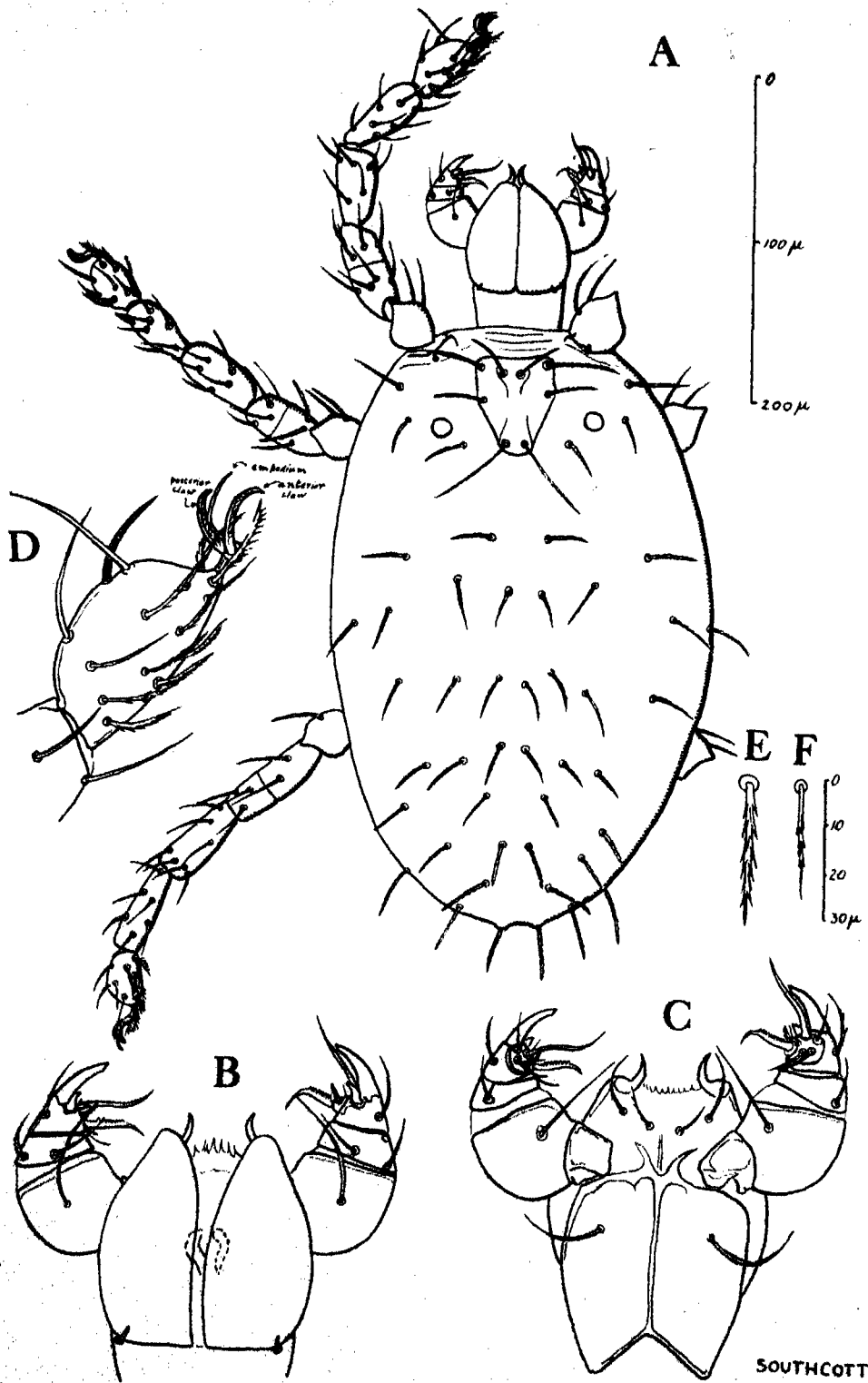
Fig. 3.—*Hauptmannia oitapensis*, n. sp. Larva. A, Dorsal view (mouthparts restored);
B, Capitulum, dorsal view (mandibles distorted and separated by compression); C, Same, below;
D, Tarsus I, anterior aspect; E, Dorsal seta; F, Ventral seta (both E and F are to the scale
shown alongside).
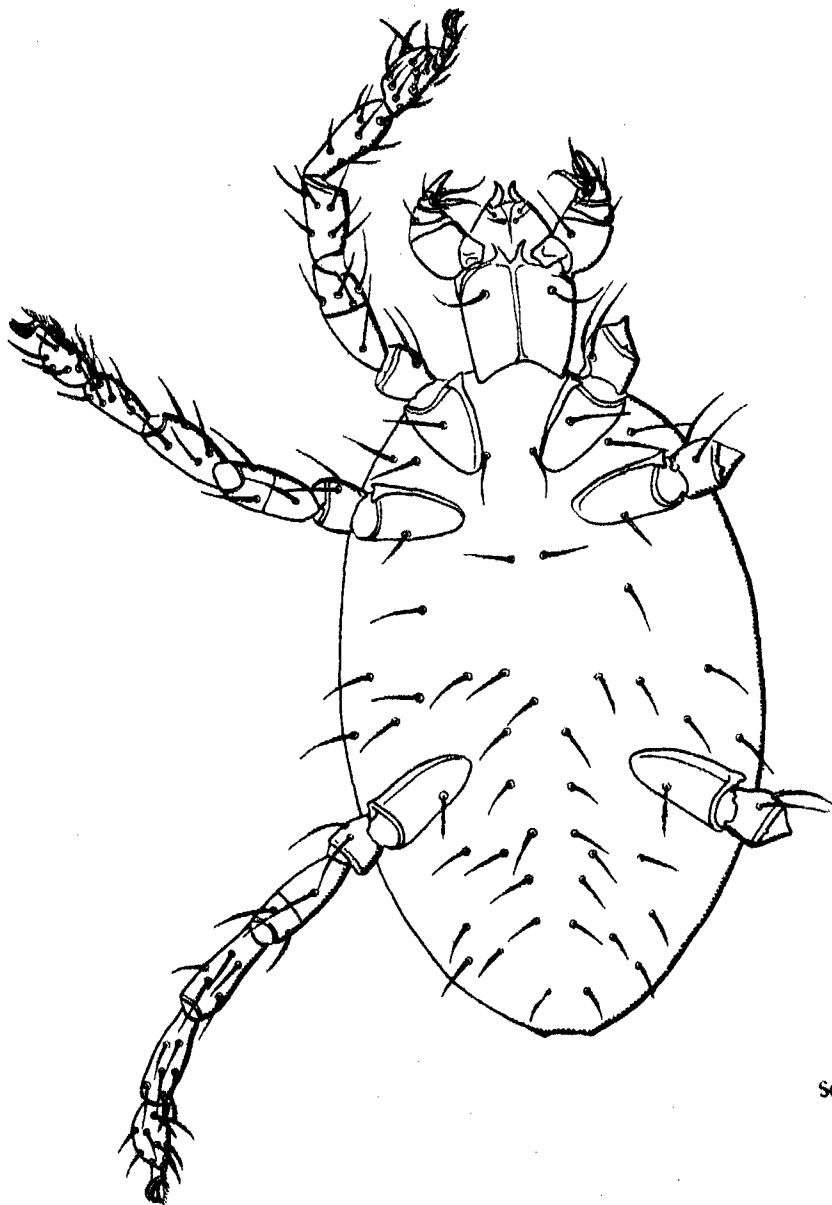
Fig. 4.—*Hauptmannia aitapensis*, n. sp. Larva, ventral view.

setae, including a pectinate seta similar to that described for the genotype, also a solenoidal spine (see Fig. 3, B, C).

Locality: Dein Creek, in the Aitape region of New Guinea, a single specimen (Type), 30th December, 1944 (R.V.S.).

Type in the author's collection (ACA 1373).

Remarks: This species is quite close to the genotype, *H. longicollis* (Ouds. 1910) from Holland.
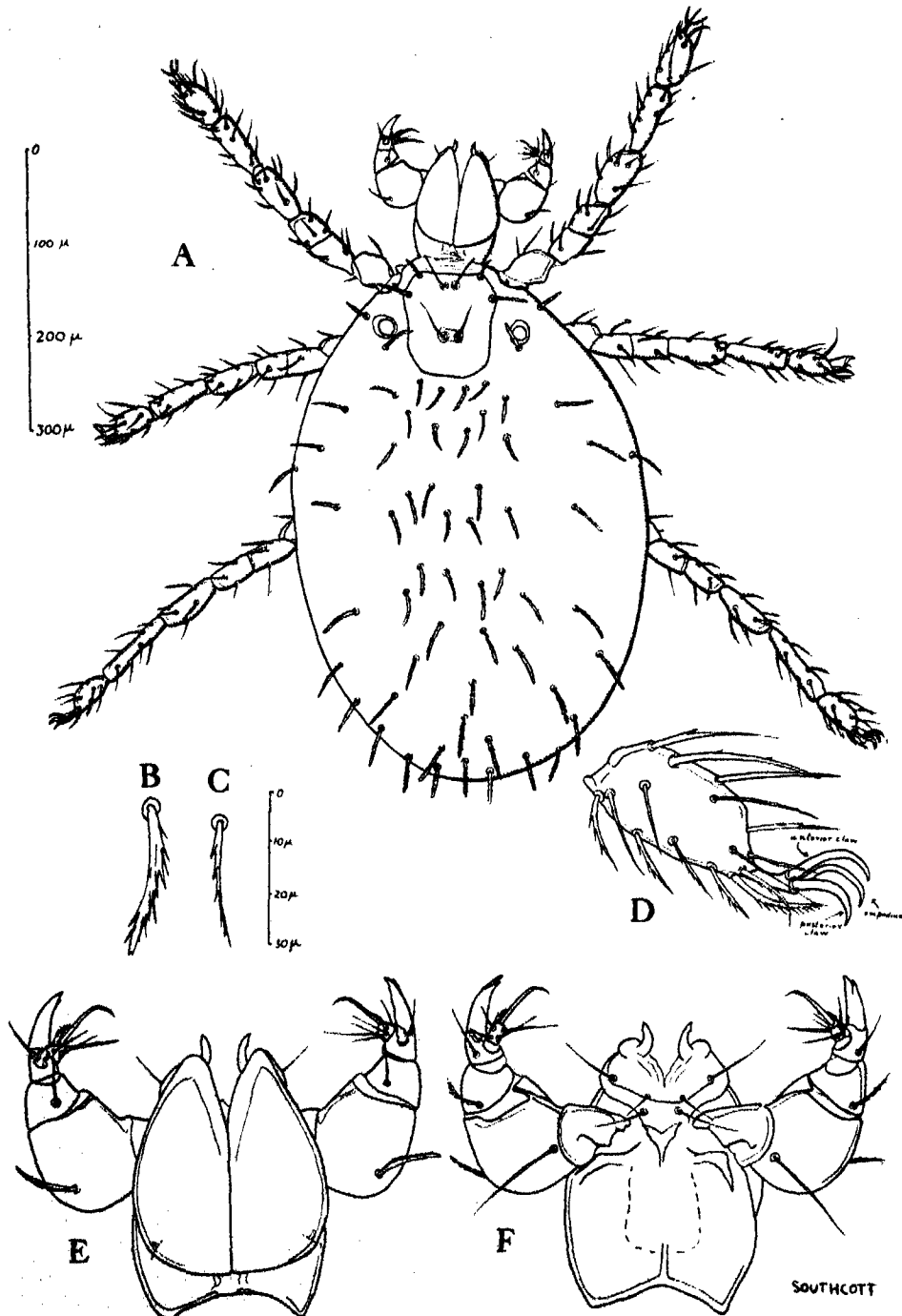
Fig. 5.—*Hauptmannia westraliensis* Wom. 1934. Larva. A, Dorsal view, entire; B, Dorsal seta; C, Ventral seta (both B and C are to the scale shown); D, Tarsus III, posterior aspect; E, Capitulum, dorsal aspect, slightly distorted by compression (the mandibles have separated anteriorly); F, Same, below.

HAUPTMANNIA WESTRALIENSIS Womersley 1934. Fig. 5, A–F; Fig. 6.

Rec. S. Aust. Mus., 1934, 5 (2): 249.

Re-description of Larva (Type): Colour not recorded, probably red. Body ovoid, 550μ long by 380μ wide (over-all length of the Type specimen, from tip of chelicerae to posterior end of abdomen is 700μ). Dorsal scutum roughly rectangular, 118μ long by 100μ wide; its anterior margin is concave, the short anterolateral margins are straight, extending from the anterior scutal non-sensillary setae to the posterior, behind this the lateral margins run almost straight backwards until they finally curve sharply
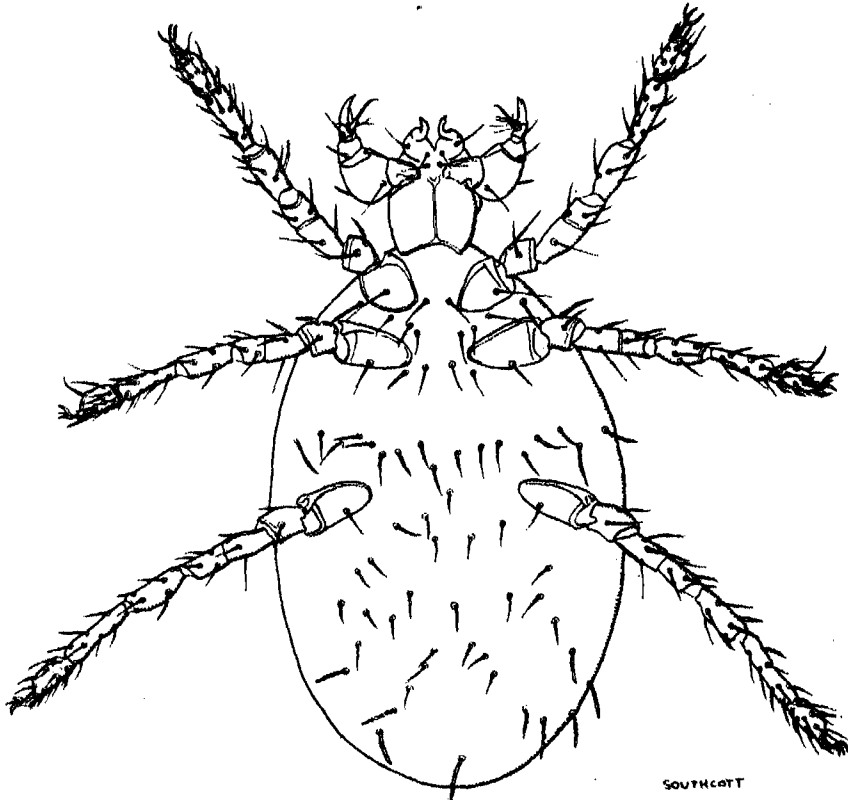
Fig. 6.—*Hauptmannia westraliensis* Wom. 1934. Larva, ventral view, entire.

medially, to run into the almost straight posterior border of the shield. Shield with 2 pairs of slender, pointed, lightly ciliated sensillary setae, anterior 39μ long, the posterior pair 43μ long, and these latter arising in a crescentic thickening in the shield; distance between centres of anterior and posterior sensilla, 41μ. Scutal non-sensillary setae are short, stout, strongly ciliated, anterior 28μ long, posterior 40μ long. Anterior sensillary setae arise between the levels of the anterior and posterior pairs of non-sensillary setae; posterior sensillary setae arise behind the middle of the shield. Shield porose. Eyes one on each side, lateral to the shield. Dorsum with about 60 stout, blunted, unpigmented, strongly ciliated setae, 26–49μ long, the more posterior setae being the longer. Venter: between coxae I a pair of slightly curved spiniform setae 30μ long; between the levels of coxae I and II is a row of 8 spiniform setae with light ciliations; just behind coxae II a further row of 4 such setae; anterior to coxae III an irregular row of 17 setae, the central setae of this row spiniform with light ciliations, the more lateral setae more heavily ciliated, and the lateralmost 2 setae of the row quite heavily ciliated and 39μ long; between and behind coxae III are about 32 setae, arranged in irregular rows, these setae becoming longer and more heavily ciliated

towards the posterior pole of the venter; ventral setae 24–40μ long. Each coxa with one seta, spiniform, faintly ciliated; on I 54μ long, on II 37μ, on III 30μ. Legs fairly strong, I 400μ long, II 395μ, III 450μ (all including coxae and claws). Each trochanter with 2 setae. Tarsi of legs short; tarsus I 53μ long by 30μ high (exclusive of claws and columella). Dorsal setae of tarsus I almost spiniform, with only a few sparse ciliations, ventral setae ciliated; solenoidal spine present on dorsum of tarsus I and II, not on III. Tarsal claws falciform, strong, simple, identical; empodium falciform, slender. Metatarsi stout, clavate; metatarsus I 72μ long. Capitulum: mandibles compact; chelicerae normal, with a short spur at the posterior end of the cutting edge. Basis capituli posterior to the palpal coxae devoid of setae. Palpi strong, short. Palpal coxa, femur, genu, tibia, tarsus with 0, 2, 2, 2, 8 setae respectively. Palpal tibia with a strong bifurcate claw, the minor tooth being on the ventrolateral aspect; a stout accessory peg to the claw also arises from the palpal tibia, on its dorsomedial aspect. Palpal tarsus with various (8) sensory setae, including a solenoidal seta, but without a pectinate seta.

Locality: "Chittering, Western Australia, October 16th, 1931, under stones" (H.W.) (slide labelled 10/10/31). A single specimen only. Type, in the South Australian Museum.

HAUPTMANNIA MULLEWAENSIS Womersley 1934.   Fig. 7, A–C; Fig. 8, A–D.

Rec. S. Aust. Mus., 1934, 5 (2): 250.

Re-description of Larva (Type): Colour not recorded, probably red. Body ovoid, 915μ long by 675μ wide (over-all length of the Type specimen, from tip of chelicerae to posterior end of abdomen is 1040μ). Dorsal scutum somewhat heart-shaped, or shaped like a traditional shield, pointed posteriorly and waisted about the middle, 252μ long by 190μ wide in front of its constriction, 201μ wide behind the constriction, and 165μ wide at the constriction. Anterior border of shield slightly concave; anterolateral borders straight; the lateral borders are sinuous and in their posterior part sweep together to meet in a blunt, rounded point. Shield with 2 pairs of filiform sensillary setae with slender ciliations, anterior pair 68μ long, posterior 47μ long; with 2 pairs of long, blunted, strongly-ciliated non-sensillary setae, anterior 58μ long, posterior 58μ long; distance between centres of anterior and posterior sensilla 60μ. The anterior sensillary setae arise behind the level of the anterior non-sensillary setae; the posterior pair of sensillary setae arises a little anterior to the waist of the shield, and well anterior to the middle of the shield. The shield is porose, but in addition the posterior half of the shield is striated, the striations being most marked peripherally; a few striations lead back from the sides of the anterior part of the shield, and run into the main striated area; the striations tend to radiate from two small thickenings in the shield. Dorsum with about 47 stout, blunted, unpigmented, strongly-ciliated setae, 28–45μ long, the more posterior setae being the longer. The setae are arranged: 1 (or 2 teratologically) anterolateral to the eye, 1 posteromedial to the eye, then rows behind the shield of 5, 6, 6, 10, 8, 4, 3, 1 (the last 2 rows being confused). Venter: between the levels of coxae I and II a row of 8 setae, spiniform with a few ciliations, the 2 most medial setae being the most anterior of the row and 68μ long, the other setae 24–58μ long; just behind coxae II a row of 6 similar setae; anterior to coxae III a row of 13 setae; between and behind coxae III the setae of the venter are arranged 2, 2, 6, 2, 6, 5, 3; the most posterior of the ventral setae are the more strongly ciliated. The spiniform ventral setae are 42–80μ long; the more heavily ciliated setae towards the posterior pole are 32–36μ long. On the ventral surface, between the last row of 2 setae in the list of ventral setae just given, is a chitinous porose pyriform plate, the precursor of the anus. Coxa I with one long spiniform seta 83μ long; coxa II with a somewhat more ciliated seta arising near its posterior border, 54μ long, and a further seta, stouter, tapering, pointed, strongly ciliated, 39μ long, arising from near the lateral end of the anterior border of the coxa; coxa III with 2 setae, placed as in coxa II, the postero-medial spiniform, almost unciliated, 54μ long, the lateral seta ciliated, similar to the lateral seta on II, but has its terminal part broken off on each side in the Type specimen.

A

B

C
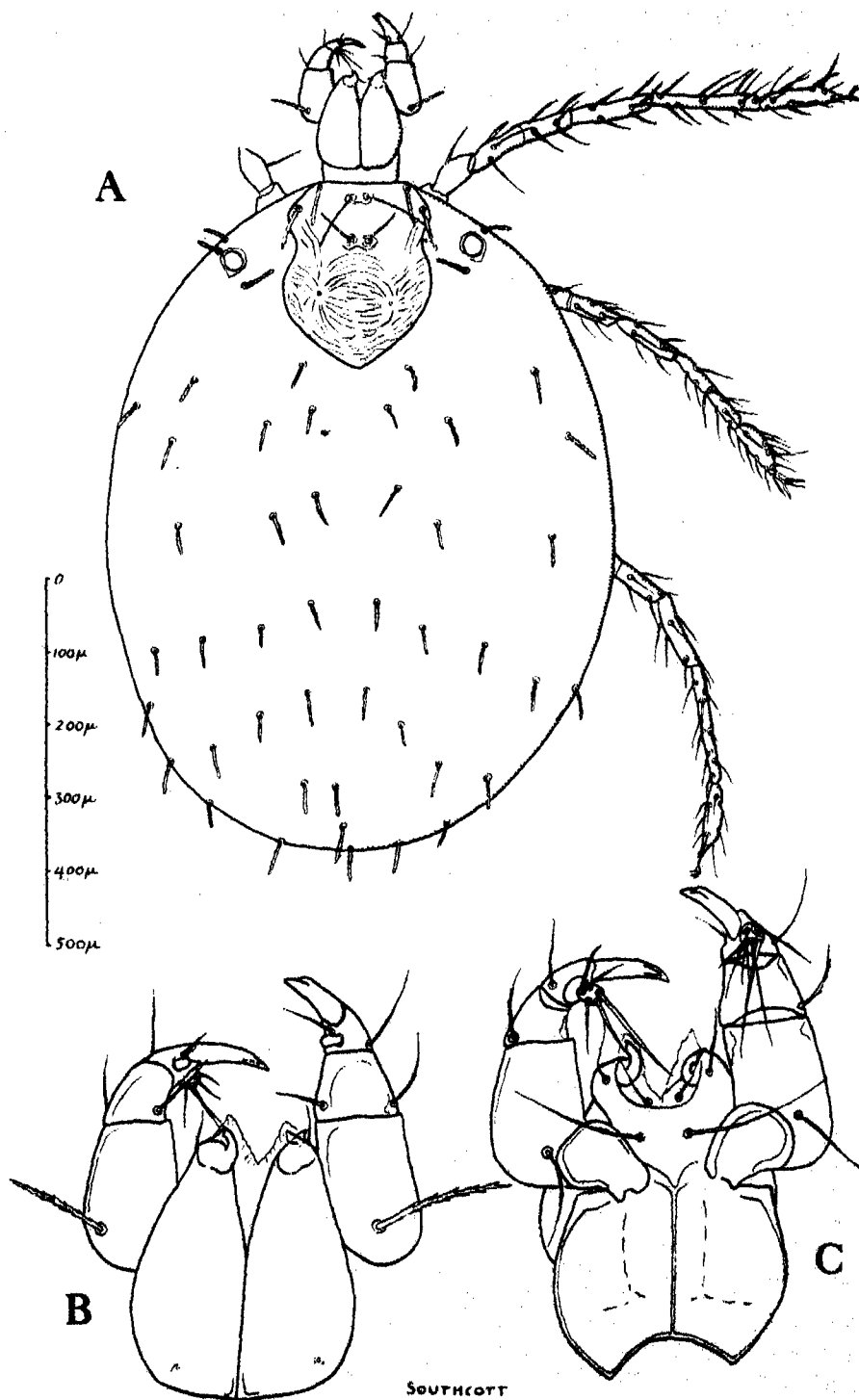
Fig. 7.—*Hauptmannia mullewaensis* Wom. 1934. Larva. A, Dorsal view; B, Capitulum, dorsal aspect, slightly distorted by compression (the mandibles have separated anteriorly); C, Same, below.

Legs comparatively thin, I 635µ long, II 610µ, III 680µ (all including coxae and claws). Each trochanter with 2 setae. Tarsus I 98µ long by 26µ high (exclusive of claws and columella). Dorsal setae of tarsus unciliated, ventral setae ciliated. Solenoidal spine present on the dorsum of tarsus I and II, not on III. Claws of tarsus falciform, strong, simple, identical; empodium falciform, more slender. Capitulum: mandibles compact; chelicera with a short spur at the posterior end of the cutting edge. Palpi strong, compact. Basis capituli posterior to palpal coxae is devoid of setae. Palpal coxa, femur,
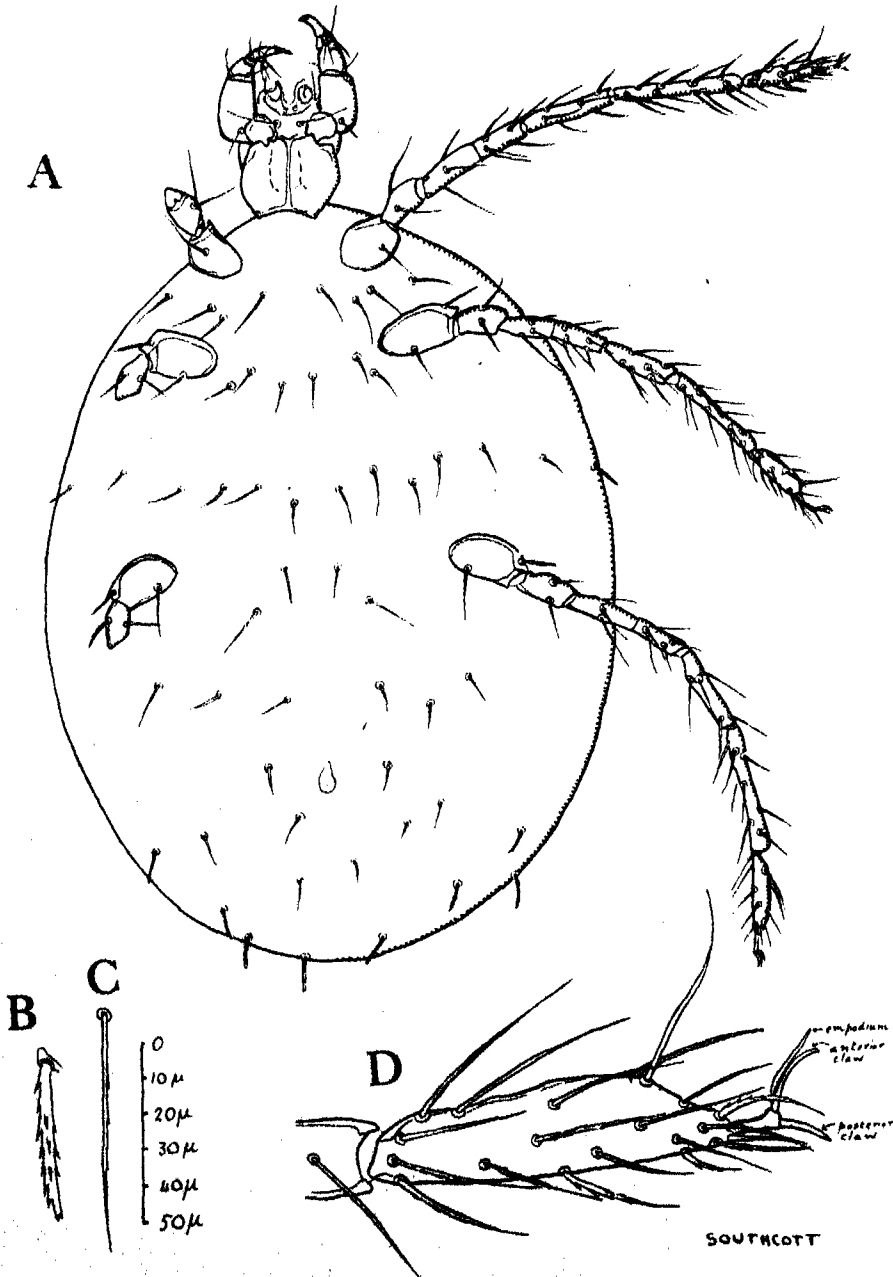
Fig. 3.—*Hauptmannia mullewaensis* Wom. 1934. Larva. A, Ventral view; B, Dorsal seta; C, Ventral seta (B and C to scale shown); D, Tarsus I, anterior aspect.

genu, tibia, tarsus with 0, 2, 2, 2, 8 setae respectively. Palpal tibia with a strong bifurcate claw, the lesser tooth being on the ventrolateral aspect; a stout accessory peg to the claw arises from the palpal tibia on its dorsomedial aspect. Palpal tarsus with 8 setae, including a solenoidal seta but without a pectinate seta.

Locality: Mullewa, Western Australia, September, 1931, on herbage (H. Womersley), a single specimen, Type.

Type in the South Australian Museum.

Remarks: This is the most divergent of the species referred to the genus.

REMARKS ON THE GENUS HAUPTMANNIA.

All the species referred to the genus in this paper have important points in common; these points are indicated in the key to the genera and the re-definition of the genus given earlier. The two European species form a compact group with *H. aitapensis*, n. sp. from New Guinea, while the two Western Australian forms diverge. The writer is not in favour of founding further genera until the adults of some at least of these species are known. It must be remembered that the status of this genus (and of *Clipeosoma* as well) as belonging to the Smarididae is as yet unproven.

ACKNOWLEDGEMENTS.

REFERENCES.

OUDEMANS, A. C., 1910.—*Ent. Ber.*, 3 (51) : 31.
————, 1910.—*Ibid.*, 3 (52) : 48-49.
————, 1910.—*Ibid.*, 3 (56) : 109.
————, 1912.—*Zool. Jahrb.*, Suppl. 14, Pt. 1 : 181-187.
SOUTHCOTT. R. V., 1946a.—*Proc. Linn. Soc. N.S.W.*, 70 (3-4) (for 1945) : 173-178.
————, 1946b.—*Ibid.*, 71 (1-2) : 6-48.
WOMERSLEY, H., 1934.—*Rec. S. Aust. Mus.*, 5 (2) : 242-250.
———— and SOUTHCOTT, R. V., 1941.—*Trans. Roy. Soc. S. Aust.*, 65 (1) : 65-68.

NITROGEN-FIXATION IN LEGUMINOUS PLANTS. VII.

THE NITROGEN-FIXING ACTIVITY OF ROOT NODULE TISSUE IN MEDICAGO AND TRIFOLIUM.

By H. L. Jensen, Macleay Bacteriologist to the Society.
(*From the Department of Bacteriology, University of Sydney.*)

(One Text-figure.)

[Read 29th October, 1947.]

INTRODUCTION.

Although the problem of symbiotic nitrogen fixation by leguminous plants and root nodule bacteria has been studied in great detail for nearly sixty years, we still know comparatively little about the quantitative side of this process, expressed as the amount of nitrogen fixed in unit time per unit of root nodule substance, and hardly anything about the influence of environmental factors on the degree of nodule-efficiency thus expressed. One reason for this is the fact that comparatively few investigators have made separate determinations of total dry matter and nitrogen in the root nodules and the rest of the plants separately, while most have contented themselves with analysing the roots and nodules together, or the tops only.

Wozak (1929) concluded from field experiments with seven species of legumes that nitrogen was fixed at a rate of 36 mgm. (in *Vicia faba*) to 98 mgm. (in *Pisum sativum*) per gm. dry nodule substance per day. He pointed out that these values are only approximate (actually somewhat too high) because they include an unknown amount of combined nitrogen taken from the soil.

Bond (1936) estimated that nodules of soy beans grown in sand fixed 24–28 mgm. nitrogen per gm. dry matter per day in young plants, and 7–8 mgm. or less in older plants. Similar figures for nodules of soy beans in sand culture were calculated by Wilson (1940) on the basis of experiments described elsewhere (Wilson and Umbreit, 1937). Earlier experiments by Whiting (1915), who recorded only the nitrogen contents and not the dry weights, suggest a similar activity of nodules in soy beans and cowpeas. Nodules of soy beans grown in water culture (Bond, 1941, Table 1) show a lower activity; a calculation according to Bond's formula (1936) indicates a fixation of only 4 mgm. nitrogen per gm. dry nodule substance per day from 29th July to 7th September, 1940. The figures given by Glöbel (1926) in his Tables 36 and 37 permit a similar calculation of the activity of nodules of soy beans grown in sand with varying doses of combined nitrogen. If we assume that the nodules, of which only the fresh weights are given, contain 20% dry matter, we find during the period from 8 to 12 weeks a daily fixation of 7·2–10·9 mgm. nitrogen per gm. dry nodule matter, falling to 5·8 mgm. with the highest dose of nitrate. Unfortunately the experiment did not include plants grown entirely with free nitrogen.

Chen and Thornton (1940) estimated that the active bacterial tissue in nodules of red clover fixed 3·90–4·59 mgm. nitrogen per cubic centimetre per day. It may be assumed (Bond, 1941) that the bacterial tissue accounts for roughly one-half of the whole nodule, and that this contains 20% dry matter of unity specific gravity; the fixation would then correspond to 9·8–11·5 mgm. nitrogen per gm. dry matter per day, a value only about one-fifth of what Wozak (1929) observed in the same species (55 mgm.). In soy bean nodule tissue Chen and Thornton found an even lower value.

There are some other experimental records from which we may calculate the overall fixation of nitrogen during the whole growth period per gm. dry nodule matter at the

end of the experiment. Jones and Tisdale (1921) found that the largest mass of nodule substance in soy beans, both absolutely and in proportion to the weight of the plant, developed at 21–24°C., but the highest actual yields of nitrogen were found at 27–30°C. Their data show also that the gain of nitrogen per gm. dry nodule increases with the temperature, from 814 mgm. at 21°C. to 2271 mgm. at 36°C. These figures, like Wozak's (1929), are only approximate, because they include some combined nitrogen taken from the soil.

From the data of Virtanen (1928) on peas and three species of clover grown in sand we may calculate the following gains of nitrogen in mgm. per gm. dry nodule matter:

Pisum sativum	994–2423 mgm.
Trifolium pratense	1484–2073 ,,
,, *repens*	1222–1702 ,,
,, *hybridum*	2324–4364 ,,

These figures show no correlation with the reaction of the sand medium (pH 5·0, 5·5 and 6·0). On the other hand, a series of experiments by the present author (Jensen, 1943) with lucerne and subterranean clover in sand and soil of varying reaction showed that the proportional weight of the nodules was generally higher, but the gain of nitrogen per gm. dry nodule substance lower, at pH 4·9–6·2 than at pH 6·7–7·5. The same observation was made in a later experiment with subterranean clover (Jensen, 1944).

Beside the fact that the species of plants and the range of reaction were not the same in Virtanen's and my own experiments, and that no allowance was made for the uptake of combined nitrogen from the medium, it was later observed (Jensen, 1946) that a partial molybdenum deficiency tends to lower the efficiency but to increase the proportional weight of the root nodules in lucerne. Experiments by Stephens and Oertel (1943), Lewis (1943), Oertel et al. (1946), and Anderson and Oertel (1946), have shown consistently that the availability of molybdenum depends on the reaction of the soil, and that its uptake generally increases with increasing pH. It is thus possible that my earlier results do not express only the direct effect of pH on the activity of the nodules, but also an indirect effect through its influence on the availability of the small amounts of molybdenum present.

New experiments have therefore been performed under conditions that should give a better understanding of the influence of reaction on the nitrogen-fixing efficiency of the root nodules. The possibility of partial molybdenum deficiency at the lower pH-ranges was ruled out by giving an adequate supply of this element, corrections were made for the combined nitrogen taken from the medium, and in most experiments the plants were harvested at several successive stages of growth. Comparative tests with plants given combined nitrogen were included in some cases.

METHODS.

Lucerne (*Medicago sativa*, var. "Giant Upright") and subterranean clover (*Trifolium subterraneum*, var. "Mount Barker"), beside barrel medic (*M. tribuloides*) and white clover (*T. repens*) in a preliminary test, were grown in glazed earthenware pots of 6 in. diameter, holding 3 kgm. sand. Unless otherwise stated, a river sand of medium coarseness and pH 5·8–5·9 was used, with an acid nutrient solution; neutral or faintly alkaline reaction was produced by adding 0·1 or 0·2% calcium carbonate to the sand. Twelve to fifteen seeds, inoculated with effective strains of the appropriate root nodule bacteria, were sown, and after germination the seedlings were thinned to (usually) six or eight per pot. The surface of the sand was covered with a mulch of clean, coarse gravel in order to reduce evaporation and growth of algae. The pots were kept in a greenhouse and arranged in randomized blocks. The moisture content of the sand was kept as near as possible to 12% of the weight of the sand, normally by watering with distilled water; during periods of maximum evaporation it was sometimes necessary to use the local tap water which contains very little lime and did not seem to affect the reaction of the sand appreciably.

At harvesting, watering was omitted for a few days previously, the plant tops were cut off at the surface, the gravel mulch was removed, and the roots were separated from the damp sand by gentle shaking and screening through a wide-meshed sieve from which the loose root-fragments were collected as completely as possible. Some loss of small rootlets was unavoidable, but it is unlikely to represent any significant proportion of the total plant-substance. The roots from each pot were placed in a dish with water and cautiously separated from each other, and the nodules were counted on each individual root system, picked off, dried, and weighed. Nodules detached during the separation of the roots were divided between the plants in that pot. The roots were kept in a refrigerator at 3–5°C. between harvest and removal of the nodules. In this way the plant material from each pot was divided into the three fractions of tops, roots, and root nodules, which were dried at 96–98°C., ground finely, and analysed for total nitrogen by the Kjeldahl method. Materials from replicate pots, of which there were usually three, were combined for analysis.

The theoretically best estimate of the amount of combined nitrogen derived by the plants from the sand would have been furnished by a series of control pots with nodule-free plants harvested at the same time as each set of inoculated plants, but this was not technically possible. As a second choice the amounts of nitrate and ammonia formed in unplanted pots, with and without calcium carbonate, were determined at intervals corresponding to the harvests. The method of Richardson (1938) was used, on somewhat larger samples of sand, usually 200 gms. The quantities of $(NO_3 + NH_4)$–N found after 8 to 18 weeks varied in the commonly used sand between 0·5 and 4·5 p.p.m., or 1·5–13·5 mgm. per pot. This plus the nitrogen content of the seed was subtracted from the gross nitrogen content of the plants to give the net gain of nitrogen. The "mobilizable" nitrogen appeared to be a fairly reliable measure of the amount of combined nitrogen becoming available, since similar quantities of nitrogen (6·2–13·3, average 10·8 mgm.) were found in wheat plants grown for 80 days in sand without addition of nitrogenous nutrients.

EXPERIMENTAL.

Preliminary Experiments.—Four species of legumes were grown in acid and alkaline sand and harvested only once, as in earlier experiments (Jensen, 1943). Lucerne and subterranean clover, ten plants per pot, were sown on 9th August, 1943, and harvested after 86 and 106 days, respectively. The nutrient solution contained 0·25 gm. KH_2PO_4; 0·25 gm. $CaCl_2$; 0·1 gm. $MgSO_4$; 0·05 gm. $FeCl_3$; and 2·5 mgm. $MnSO_4$, $ZnSO_4$, $CuSO_4$, Na_2MoO_4, and $Na_2B_4O_7$, all per pot; the last five constituents are in the following collectively referred to as "minor salts". The alkaline sand was given 0·2% $CaCO_3$. In this series alone the pots contained only 2·5 kgm. sand, and there were only duplicate pots of subterranean clover. Barrel medic and white clover were sown on 27th August, 1943, and harvested after 80 and 101 days. The results are seen in Table 1. In this and subsequent tables the significance of differences between yields at acid and alkaline reaction is expressed by the t-test (Fisher, 1946). Where only two yields are compared, the degree of significance is shown by the following symbols:

$$+ \quad : P = 0·05–0·02$$
$$+ + \quad : P = 0·02–0·01$$
$$+ + + \quad : P < 0·01$$

When more than two means are compared, the differences necessary for significance at the five, two and one per cent. points (P = 0·05, 0·02 and 0·01) are stated.

The figures show that only in *Medicago tribuloides* is the gain of nitrogen, actual as well as per gm. dry nodule, significantly lower at acid reaction. In the other plants the variation between replicate pots was considerable, and the gains of nitrogen are not significantly different, except that the gain per gm. dry nodule in subterranean clover is slightly higher at alkaline reaction. As found before (Jensen, 1943), the average numbers of nodules on lucerne and barrel medic are much lower in acid than in alkaline sand, but the weight of the whole nodule-fraction is less strongly affected, owing to a larger average size of the nodules in acid sand. Text-fig. 1 shows two selections of typical

TABLE I.

Nitrogen Fixation by Four Species of Leguminous Plants in Acid and Alkaline Sand.

		Lucerne.		Subterranean Clover.		Barrel Medic.		White Clover.	
pH of sand, initial		5·7	7·2	5·7	7·2	5·0	7·4	5·0	7·4
„ „ „ final		4·7–4·8	7·1–7·3	4·3–4·4	7·2–7·3	4·8–5·2	7·5–7·6	4·3–4·5	7·6–7·8
Dry matter,	Tops	3·52	3·78	6·06	7·62	1·68	7·07	4·96	5·98
gm. per pot,	Roots	3·12	3·53	1·23	1·71	0·37	1·37	0·88	1·03
mean.	Nodules	0·130	0·145	0·309	0·344	0·095	0·132	0·105	0·125
Percentage of N in	Tops	3·03	3·06	2·22	2·40	2·23	2·45	2·25	2·78
dry matter.	Roots	2·07	2·04	2·35	2·34	1·60	2·24	2·27	2·06
	Nodules	6·14	8·33	6·43	7·34	3·61	5·40	5·82	5·30
Total N in plants, mgm.		178·9	198·2	183·1	248·1	47·1	211·0	137·4	194·0
Net gain of N, mgm.		176·2	193·7	175·9	239·1	38·7	204·1	131·0	189·1
Do. per gm. dry nodule-substance		1360	1352	569	698	407	1598	1248	1513
Nodules per plant.	Mean	11·7	62·3	65·7	49·6	10·5	36·2	64·8	77·3
	S.E.*	±0·90	±4·24	±4·86	±2·96	±1·68	±2·76	±6·96	±7·30
Significance of differences between: Net gains of N		—		—		+++		—	
Do. per gm. dry nodule-substance in acid and alkaline sand		—		+		+++		—	

* S.E. = standard error, expressed as the standard deviation divided by the square root of the number of plants.

nodules from lucerne. In the two clovers the reaction has little effect on either the numbers or the aggregate weight of the nodules; subterranean clover even shows a slightly but significantly higher mean number in acid sand.

The acidity of the acid sand increased strongly during the growth period. The clovers even acidified the sand to pH 4·3–4·4 without the gains of nitrogen being significantly lowered.

Another preliminary experiment was designed to show at what pH-level the effect on nodule numbers and nitrogen fixation becomes significant. A fine yellow hill sand
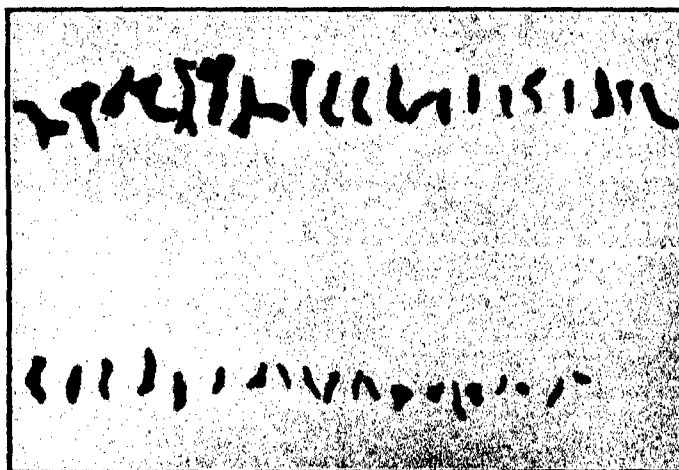
Fig. 1.—Selections of typical nodules from lucerne grown for 86 days in acid sand (above) and alkaline sand (below). (S. Woodward-Smith photo.) × approximately ⁴/₃.

was adjusted to four ranges of reaction by addition of increasing doses of calcium carbonate besides a nutrient mixture of 0·5 gm. KH_2PO_4; 0·5 gm. $CaSO_4$; 0·25 gm. $MgSO_4$; 0·25 gm. NaCl; 0·1 gm. $FeCl_3$; and 3 mgm. of the minor salts. Lucerne and subterranean clover, eight plants per pot, were sown on 31st July and 27th August, 1944, respectively, and harvested after 140 and 108 days.

As shown in Table 2, the net gains of nitrogen by lucerne are not significantly influenced by the reaction, even at pH initially below 5, but the gain per gm. dry nodule is at this reaction significantly lower than at the three other pH-levels. Nodules are still formed at pH (initially) 4·7-4·9, which is below the pH-limit for nodule formation in agar culture (Jensen, 1943), but the numbers of nodules show a marked increase between the pH-levels of 5·4-5·5 and 6·3-6·6. The results thus confirm the earlier observation that the activity of nodules already formed is much less sensitive to acidity than is the formation of new nodules.

TABLE 2.

Nitrogen Fixation by Lucerne and Subterranean Clover at Four Ranges of Reaction.

		Lucerne (31/7/44-18/12/44).				Clover (28/7/44-13/11/44).			
% $CaCO_3$ added		0	0·01	0·04	0·4	0	0·01	0·04	0·4
pH of sand, initial		4·7-4·9	5·4-5·5	6·3-6·6	7·0-7·1	4·5	4·8-4·9	6·0-6·3	6·7-6·8
" " " final		4·3-4·5	5·0-5·1	6·9-7·2	7·6-7·7	4·1-4·3	4·5-4·7	6·2-6·4	7·6-7·7
Dry matter,	Tops	6·20	7·22	7·22	8·33	5·35	5·68	5·27	5·17
gm. per pot,	Roots	5·75	5·05	5·78	6·02	0·94	1·21	1·08	1·03
mean.	Nodules	0·148	0·088	0·101	0·106	0·157	0·146	0·152	0·208
Percentage of N	Tops	2·68	2·84	2·35	2·78	3·05	3·05	2·61	2·56
in dry matter.	Roots	2·32	2·49	2·37	1·38	3·24	2·58	2·92	2·59
	Nodules	7·44	6·90	7·20	6·81	7·12	7·83	6·82	6·52
Total N in plants, mgm.		309·9	339·5	313·9	325·3	205·1	215·9	181·9	171·2
Net gain of N, mgm.		278·6	308·2	288·3	299·7	170·2	181·0	156·3	145·6
Do. per gm. dry nodule-substance		1939	3539	2874	2846	1112	1236	1010	722
Nodules per plant.	Mean	18·4	25·2	57·2	50·4				
	S.E.	±2·37	±4·63	±4·47	±5·32				

	Significant difference at P =			Significant difference at P =		
	0·05	0·02	0·01	0·05	0·02	0·01
Net gain of N	52·1	65·5	75·9	96·4	121·2	140·3
Do. per gm. dry nodule-substance	692	870	1004	351	441	511

The net gains of nitrogen in clover, although rather low and irregular, are also unaffected by the reaction, but the gain per gm. dry nodule shows a significant decline at the highest pH-level. The nodules were not counted in this case. The results are hardly altogether conclusive, because the plants suffered badly from attack by mites, but they do confirm the observation that subterranean clover can fix nitrogen in sand of pH 4·1-4·5. No further experiments were undertaken with this sand, for reasons explained below.

Main Series of Experiments with Lucerne.

Experiment No. 1.—Lucerne was sown on 28th February, 1944, eight plants per pot, and harvested after 64, 92 and 120 days. The nutrients consisted of 0·5 gm. KH_2PO_4; 0·1 gm. K_2HPO_4; 0·6 gm. $CaCl_2$; 0·3 gm. $MgSO_4$; 0·03 gm. $FeCl_3$; 3·0 mgm. minor salts; and 0·1% $CaCO_3$ in the alkaline sand. The results in Table 3 show that neither the actual gains of nitrogen nor the gains per gm. dry nodule are significantly different at the two ranges of reaction, even at the final harvest when the pH of acid sand has fallen well below 5. The numbers of nodules are, especially in the early stages, much lower

in the acid sand, but their aggregate weight is practically unaffected by the reaction, and their activity shows no clear-cut change with increasing age.

Experiment No. 2.—The acid hill sand was used, with the following nutrients: 0·4 gm. KH_2PO_4; 0·1 gm. K_2HPO_4; 0·5 gm. $CaSO_4$; 0·25 gm. $MgSO_4$; 0·1 gm. $FeCl_3$; 3·0 mgm. minor salts; and 0·1% $CaCO_3$ in the alkaline sand. Lucerne, eight plants per pot, was sown on 25th August, 1944, and harvested after 60, 85 and 100 days. Table 4 shows the results. The sand without calcium carbonate rapidly becomes strongly acid; the net gains of nitrogen are significantly lower than in the faintly alkaline sand, and the gain per gm. dry nodule shows a very marked reduction at the final harvest. This confirms the former observation (Table 2) that an acidity of pH 4·5–4·8 is too high for

TABLE 3.

Nitrogen Fixation by Lucerne, Experiment No. 1 (28/2/44–27/6/44).

Treatment.	Days.	pH of Sand.	Dry Matter, gm.			% N in Dry Matter.			Nodules per Plant. Mean and S.E.
			Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.	
−CaCO₃ Initial pH 5·7	64	5·0–5·7	0·55	0·14	0·012	3·29	2·12	8·02	3·4 ± 0·60
	92	5·1–5·5	1·65	0·72	0·055	3·84	2·34	6·72	21·4 ± 2·97
	120	4·6–4·8	3·99	3·26	0·142	3·72	2·05	8·87	41·8 ± 5·82
+CaCO₃ Initial pH 6·7	64	6·9–7·0	0·74	0·25	0·021	4·03	2·20	7·77	21·1 ± 2·46
	92	7·1–7·2	1·68	1·08	0·048	4·53	2·38	6·76	42·7 ± 3·09
	120	7·0–7·1	3·89	3·29	0·135	4·24	2·20	9·26	127·9 ± 16·3

Summary :

Days.	Total N in Plants, mgm.		Net Gain of N, mgm.			Gain of N, mgm. per gm. Dry Nodule-substance.		
	−CaCO₃.	+CaCO₃.	−CaCO₃.	+CaCO₃.	Significance of Difference.	−CaCO₃.	+CaCO₃.	Significance of Difference.
64	22·0	36·9	21·0	29·6	—	1750	1410	—
92	84·0	108·7	76·2	94·9	—	1380	1977	—
120	227·7	249·7	218·9	241·7	—	1541	1790	—

TABLE 4.

Nitrogen Fixation by Lucerne in Hill Sand, Experiment No. 2 (25/8/44–5/12/44).

Treatment.	Days.	pH of Sand.	Dry Matter, gm.			% N in Dry Matter.			Nodules per Plant. Mean and S.E.
			Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.	
−CaCO₃ Initial pH 5·1	60	4·8–5·0	0·34	0·14	0·012	3·54	2·18	8·04	3·5 ± 0·63
	85	4·6–4·8	2·13	1·38	0·078	4·07	2·54	7·39	9·9 ± 1·68
	100	4·5–4·6	3·61	2·72	0·123	2·88	2·36	6·54	17·7 ± 2·79
+CaCO₃ Initial pH 7·2	60	7·1–7·2	0·83	0·22	0·026	3·76	1·25	7·68	16·1 ± 0·68
	85	7·0–7·4	2·95	2·27	0·080	2·85	2·35	8·38	26·4 ± 2·49
	100	7·2–7·5	4·93	3·87	0·098	3·20	2·39	7·20	30·3 ± 3·58

Summary :

Days.	Total N in Plants, mgm.		Net Gain of N, mgm.			Gain of N, mgm. per gm. Dry Nodule-substance.		
	−CaCO₃.	+CaCO₃.	−CaCO₃.	+CaCO₃.	Significance of Difference.	−CaCO₃.	+CaCO₃.	Significance of Difference.
60	16·0	35·9	(0)	17·8			712	
85	127·3	144·2	99·0	119·8	+	1298	1506	—
100	175·1	257·7	143·8	232·1	+ +	1209	2321	+ + +

maximum nitrogen fixation, but the process still continues. The numbers and weights of nodules show the same behaviour as previously observed; the small but apparently significant increase (7·8 ± 3·26) in numbers between the 85th and the 100th day at pH 4·5–4·8 is noteworthy.

This sand had unfortunately a high content of metabolizable nitrogen and produced up to 10 p.p.m. NO_3–N, which involved an undesirably large correction for nitrogen taken from the medium (hence no gain of nitrogen in acid sand after 60 days). It was therefore not used any more except for one experiment with subterranean clover (Table 9) conducted together with the present.

Experiment No. 3.—This comprised two series, with free and combined nitrogen. The basal nutrients were 0·5 gm. KH_2PO_4; 0·5 gm. $CaCl_2$; 0·25 gm. $MgSO_4$; 0·25 gm. NaCl; 0·1 gm. $FeCl_3$; 3·0 mgm. of the minor salts; and 0·2% $CaCO_3$ in the alkaline sand. Combined nitrogen was provided as 120 mgm. as $NaNO_3$ per pot at start, and 3 × 60 mgm. as $(NH_4)_2SO_4$ after 57, 77 and 91 days; this mixture was chosen in order to minimize the pH-changes due to preferential assimilation of the nitrate- and ammonium-ions. Lucerne was sown on 23rd February, 1945, and harvested after 56, 76, 91 and 105 days, six plants per pot.

TABLE 5.

Nitrogen Fixation and Uptake of Combined Nitrogen by Lucerne, Experiment No. 3 (23/2/45–5/6/45).

Treatment.	Days.	pH of Sand.	Dry Matter, gm.			% N in Dry Matter.			Nodules per Plant, Mean and S.E.
			Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.	
Free N	56	6·0–6·2	1·07	0·38	0·042	3·59	1·94	6·82	9·6±1·53
−CaCO₃	76	5·1–5·6	3·51	2·32	0·106	3·84	2·46	7·85	17·5±1·02
Initial pH	91	5·1–5·4	4·35	3·73	0·170	3·56	2·12	7·84	42·0±5·43
5·4–5·5	105	4·9 5·4	5·28	5·45	0·178	2·92	2·01	6·85	46·0±4·46
Free N	56	7·3–7·4	1·42	0·61	0·047	3·60	2·38	6·70	21·4±1·61
+CaCO₃	76	7·6–7·8	3·11	1·73	0·095	3·20	2·23	8·02	25·6±2·41
Initial pH	91	7·2–7·3	4·55	3·76	0·148	3·89	1·83	6·92	39·3±3·72
6·8–7·0	105	7·2–7·3	5·93	6·08	0·176	3·40	2·21	6·79	53·0±6·99
Comb. N	56	6·8–7·0	2·27	0·98	0·018	3·60	2·22	6·01	17·5±2·62
−CaCO₃	76	5·6–6·0	4·31	3·73	0·095	2·75	2·10	7·25	38·8±3·09
Initial pH	91	4·7–5·1	5·24	4·93	0·094	3·47	2·28	7·75	32·0±3·36
5·4–5·5	105	4·9–5·0	7·17	6·78	0·139	3·28	2·08	7·19	37·3±3·97
Comb. N	56	8·1–6·2	2·17	0·86	0·016	3·55	2·30	7·10	17·2±2·99
+CaCO₃	76	7·6–7·8	4·69	3·62	0·097	2·95	1·94	8·84	29·8±2·89
Initial pH	91	7·0–7·4	5·15	4·84	0·084	3·30	2·08	6·72	50·6±7·32
6·8–7·0	105	7·2–7·3	6·52	6·77	0·100	3·12	2·08	7·04	44·3±3·83

Summary : Free-nitrogen series.

Days.	Total N in Plants, mgm.		Net Gain of N, mgm.			Gain of N, mgm. per gm. Dry Nodule-substance.		
	$-CaCO_3$.	$+CaCO_3$.	$-CaCO_3$.	$+CaCO_3$.	Significance of Difference.	$-CaCO_3$.	$+CaCO_3$.	Significance of Difference.
56	48·9	67·7	46·3	62·2	—	1140	1345	—
76	202·4	145·3	198·1	140·8	+	1857	1612	—
91	249·7	255·9	243·8	251·8	—	1443	1706	+ + +
105	276·0	347·5	271·2	344·0	—	1516	1967	+

Summary : Combined-nitrogen series.

Days.	Total N in Plants, mgm.		Significance of Difference.	Net Gain of N, mgm. (assumed)	
	$-CaCO_3$.	$+CaCO_3$.		$-CaCO_3$.	$+CaCO_3$.
56	104·5	97·9	—	(0)	(0)
76	203·5	217·2	—	(29·1)	(47·2)
91	301·6	273·4	—	(55·7)	(29·3)
105	385·2	351·3	—	(80·4)	(47·8)

Relative Numbers and Weights of Nodules.		Acid Sand after Days.				Alkaline Sand after Days.			
		56	76	91	105	56	76	91	105
Nodules, number per gm. dry root.	Free N ..	165	45	74	58	99	93	65	59
	Comb. N ..	103	63	41	85	126	46	68	39
Weight of nodules in % of total dry matter.	Free N ..	2·78	1·76	2·07	1·63	2·22	1·79	1·75	1·46
	Comb. N ..	0·53	1·16	0·91	0·98	0·44	1·13	0·83	0·73

The results in Table 5 show that the growth with free nitrogen is somewhat irregular, and the reaction has as a whole no significant influence on the net gains of nitrogen, except after 77 days, when the gain is higher at acid reaction. The gains per gm. dry nodule at the two last stages show significantly lower values at pH 4·9–5·4 than at pH 7·2–7·3, although the difference is not very conspicuous. The numbers of nodules are in this case not significantly different at the two reactions after 91 and 105 days; a possible explanation may be that extensive infection of the roots has taken place during the first 56 days when the sand was only faintly acid, the nodules only later becoming visible to the naked eye.

The plants with combined nitrogen grew more rapidly than with free nitrogen. At no stage does the reaction significantly affect the uptake of nitrogen, but unfortunately the pH-values are very inconstant; after 56 days the sodium nitrate had almost neutralized the acid sand and rendered the sand with calcium carbonate strongly alkaline. Except at the first harvest the crops at both reactions contain more nitrogen than was added in combined form (180, 240 and 300 mgm.), and small amounts of nitrate and ammonia were found in the sand after harvest; thus the plants appear to have fixed some nitrogen in the presence of excess available nitrogen in the growth substrate, as

also observed by Glöbel (1926). An estimate of the gain of nitrogen in these pots was made by subtracting the nitrogen added to the sand, plus the mineral nitrogen produced in unplanted control sand, from the nitrogen content of the plants plus the mineral nitrogen found in the sand after harvest. These estimates are of course only tentative, *inter alia*, because of the possibility that some mineral nitrogen may disappear through microbial processes in the sand, and especially the plant rhizospheres. The gains of nitrogen per gm. dry nodule seem to range between 300 and 600 mgm., or roughly one-sixth to one-third of the corresponding values in the free-nitrogen series. The provision of combined nitrogen in a quantity comparable to the fixation by plants in nitrogen-free sand in the same time has thus strongly reduced the nitrogen-fixing efficiency of the nodule tissue, without, however, suppressing it completely. The numbers of nodules are little influenced by the reaction and are not significantly lower, after 56 and 76 days at acid reaction even higher, than in the free-nitrogen series. When the more rapid growth with combined nitrogen is taken into consideration and the number of nodules expressed on the basis of dry root weight, the numbers appear somewhat, but not constantly or markedly, lower in the presence of combined nitrogen (cf. Thornton and Nicol, 1936, and many earlier workers quoted by Fred et al., 1932). A far more striking effect of the combined nitrogen is the great decrease in the average size of the nodules, as also found by Glöbel (1926) and Thornton and Nicol (1936), and consequently in the weight of the nodule-fraction in proportion to the whole plant; this is particularly noticeable at the first harvest when the excess of combined nitrogen was highest and no nitrogen had yet been fixed.

Experiment No. 4.—Combined nitrogen was given as ammonium nitrate, in order to avoid drastic pH-changes. The basal nutrients were 0·4 gm. KH_2PO_4; 0·4 gm. $CaCl_2$; 0·2 gm. $MgSO_4$; 0·2 gm. NaCl; 0·08 gm. $FeCl_3$; 1·2 mgm. of the minor salts; and 0·1% $CaCO_3$ in the alkaline sand. The pots in the combined-nitrogen series received at first 24, later 48 mgm. nitrogen per week in two doses, so as to imitate the conditions in a vigorously nitrifying soil. Lucerne, six plants per pot, was sown on 20th July, 1945, and harvested after 35, 68, 88 and 102 days, when the combined-nitrogen pots had received 60, 192, 276 and 372 mgm. nitrogen respectively. Table 6 gives the results.

TABLE 6.

Nitrogen Fixation and Uptake of Combined Nitrogen by Lucerne, Experiment No. 4 (20/7/45–30/10/45).

Treatment.	Days.	pH of Sand.	Dry Matter, gm.			% N in Dry Matter.			Nodules per Plant, Mean and S.E.
			Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.	
Free N, —CaCO₃. Initial pH, 5·1-5·2	35	6·1-6·2	—	—	—	...	—	—	5·5±1·17
	68	5·8-6·2	0·72	0·42	0·050	3·62	2·38	6·80	12·1±1·10
	88	5·4-5·6	2·10	1·42	0·083	3·23	2·26	6·68	11·4±1·09
	102	5·3-5·6	3·61	2·89	0·164	3·11	2·23	6·57	12·8±0·90
Free N, +CaCO₃. Initial pH, 6·8-6·9	35	7·0	—	—	—	—	—	—	8·5±0·81
	68	7·2-7·5	1·11	0·62	0·064	3·42	2·00	6·56	33·8±3·71
	88	7·2-7·5	2·92	2·14	0·103	3·14	2·20	7·05	48·9±4·32
	102	7·3-7·4	4·31	3·92	0·169	2·86	2·18	6·83	51·5±6·47
Comb. N, —CaCO₃. Initial pH, 5·1-5·2	35	5·7-5·8	—	—	—	—	—	—	0·3±0·55
	68	5·1-5·2	1·42	0·79	0·011	3·82	2·64	6·07	9·9±1·52
	88	4·9-5·5	3·59	2·42	0·039	3·37	2·44	5·78	7·1±1·10
	102	4·7-5·0	5·65	5·54	0·054	2·89	2·31	4·95	6·6±1·26
Comb. N, +CaCO₃. Initial pH, 7·5-8·0	35	6·7-6·8	—	—	—	—	—	—	4·9±0·76
	68	7·5-7·7	1·05	0·92	0·011	3·62	2·57	6·00	32·0±7·14
	88	7·6-7·8	4·42	3·14	0·035	3·17	2·26	6·80	38·3±4·15
	102	7·5-8·0	6·47	5·92	0·035	2·73	2·25	6·00	27·7±3·38

Summary : Free-nitrogen series.

Days.	Total N in Plants, mgm.		Net Gain of N, mgm.			Gain of N, mgm. per gm. Dry Nodule-substance.		
	- CaCO₃.	+ CaCO₃.	- CaCO₃.	+ CaCO₃.	Significance of Difference.	- CaCO₃.	+ CaCO₃.	Significance of Difference.
35	1·7	2·9	(0)	(0)	—	(0)	(0)	—
68	39·6	54·4	37·2	51·4	—	743	808	·
88	105·4	145·5	103·0	142·5	+ + +	1241	1394	—
102	187·3	220·0	170·8	214·9	—	1097	1284	—

Summary : Combined-nitrogen series.

Days.	Total N in Plants, mgm.		Significance of Difference.
	- CaCO₃.	+ CaCO₃.	
35	2·9	2·7	—
68	76·8	94·7	—
88	182·4	213·4	—
102	293·3	311·8	—

Relative Numbers and Weights of Nodules.		- CaCO₃, after Days.			+ CaCO₃, after Days.		
		68	88	102	68	88	102
Number of nodules per gm. dry root.	Free N	184	49	27	326	144	96
	Comb. N	71	17	7	201	74	28
Weight of nodules in % of total dry matter.	Free N	4·23	2·32	2·37	3·55	2·00	2·00
	Comb. N	0·50	0·61	0·47	0·36	0·44	0·26

The growth was at first very slow, owing to a period of cold weather. Addition of nitrogen was therefore interrupted for 2½ weeks, and only total nitrogen and numbers of nodules were determined after 35 days. In the free-nitrogen series the net gain of nitrogen is after 88 days significantly lower at acid reaction, a rather unexpected result in view of the only moderately high acidity. The gains per gm. dry nodule are not significantly different, but upon the whole lower than in any other experiment. The numbers of nodules in acid sand, too, appear unusually low, which may perhaps explain the small crop yield after 88 days.

The combined-nitrogen series shows better growth, but the added nitrogen was in no case used up, and no nitrogen appears to have been fixed. The total nitrogen content of the plants is not significantly influenced by the reaction, although the acidity of the acid sand increased considerably. The actual numbers of nodules are only at the last harvest markedly lower than in the corresponding free-nitrogen pots. On the other hand the provision of combined nitrogen has greatly reduced the numbers of nodules per gm. root, especially in the acid sand. An even more conspicuous effect is seen on the proportional weight of the nodules, which is only one-tenth to one-fourth of the

corresponding figures in the free-nitrogen series. It is noteworthy that this effect of the combined nitrogen is much more pronounced in the present experiment, where a considerable excess of available nitrogen was left in the medium, than in the previous one (Table 5).

Experiment No. 5.—This was designed like the previous one, except that 1·5 mgm. of the minor salts was given and the combined-nitrogen pots received first 15 and later 30 mgm. nitrogen per week in two doses. Lucerne was sown on 31st August, 1945, and harvested after 59, 74, 88 and 102 days, when the combined-nitrogen series had received 180, 240, 300 and 360 mgm. nitrogen per pot. Table 7 shows the results.

The plants grew more vigorously than in the previous experiment, especially in the free-nitrogen series where the reaction of the sand without calcium carbonate is only moderately acid. The net gains of nitrogen are not significantly different, except perhaps at the first harvest, and the gains per gm. dry nodule are barely significantly higher in neutral than in acid sand at the first and third harvest, and generally on a high level. The nodules develop slowly in the acid sand, but at the last harvest their numbers are as high as at pH 7·0–7·5.

TABLE 7.

Nitrogen Fixation and Uptake of Combined Nitrogen by Lucerne (31/8/45–11/12/45).

Treatment.	Days.	pH of Sand.	Dry Matter, gm.			% N in Dry Matter.			Nodules per Plant, Mean and S.E.
			Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.	
Free N,	59	5·4–5·9	1·56	0·59	0·059	3·19	2·34	6·41	10·0±1·46
—CaCO₃,	74	5·3–5·6	3·47	1·93	0·091	3·30	2·46	7·36	15·7±2·01
Initial pH,	88	5·1–5·6	4·82	3·21	0·136	3·23	2·40	7·18	28·4±3·14
5·4–5·7	102	6·0–6·1	7·01	5·88	0·172	3·15	2·44	7·18	46·2±4·21
Free N,	59	7·3–7·7	2·16	0·85	0·055	3·52	2·26	6·91	26·8±2·66
+CaCO₃,	74	7·0–7·3	3·83	2·16	0·082	3·21	2·39	6·69	40·9±3·66
Initial pH,	88	7·3–7·6	5·18	3·45	0·095	2·97	2·27	8·14	41·1±3·91
7·1–7·3	102	7·0–7·5	7·33	4·68	0·129	2·98	1·99	6·93	50·7±5·66
Comb. N,	59	4·9–5·5	2·16	0·95	0·013	3·68	2·76	7·08	4·2±0·85
—CaCO₃,	74	4·9–5·0	4·75	3·34	0·051	3·00	2·40	5·54	6·9±1·26
Initial pH,	88	4·5–5·0	5·57	3·87	0·028	3·04	2·58	5·03	6·2±0·98
5·4–5·7	102	4·9–5·0	7·90	6·06	0·061	2·75	2·27	4·31	4·6±0·88
Comb. N,	59	7·1–7·7	3·56	1·86	0·033	3·41	2·25	7·07	30·6±2·81
+CaCO₃,	74	7·1–7·2	5·30	3·53	0·037	3·06	2·40	6·02	28·8±2·55
Initial pH,	88	7·5–7·6	6·60	5·59	0·040	2·86	2·34	5·98	28·5±3·42
7·1–7·3	102	7·4–7·6	8·25	7·09	0·042	2·64	2·22	5·95	30·4±2·29

Summary: Free-nitrogen series.

Days.	Total N in Plants, mgm.		Net Gain of M, mgm.			Gain of N, mgm. per gm. Dry Nodule-substance.		
	—CaCO₃.	+CaCO₃.	—CaCO₃.	+CaCO₃.	Significance of Difference.	—CaCO₃.	+CaCO₃.	Significance of Difference.
59	67·0	99·0	59·9	89·5	+	1073	1821	+
74	168·5	180·2	161·4	170·7	—	1861	2141	—
88	242·3	240·0	229·8	224·5	—	1733	2407	+
102	370·9	320·2	359·0	300·8	—	2083	2335	—

Summary: Combined-nitrogen series.

Days.	Total N in Plants, mgm.			Net Gain of N, mgm.		
	−CaCO₃.	+CaCO₃.	Significance of Difference.	−CaCO₃.	+CaCO₃.	
59	101·9	161·2	+ + +	(0)	(0)	
74	224·1	252·2	—	(0)	(26·8)	Gain of nitrogen in one pot
88	272·0	321·7	—	(0)	(31·0)	after 74 days and in two
102	357·0	377·7	—	(0)	(25·5)	after 88 and 102 days.

Relative Numbers and Weights of Nodules.		−CaCO₃, after Days.				+CaCO₃, after Days.			
		59	74	88	102	59	74	88	102
Nodules, number per gm. dry roots.	Free N ..	101	52	53	48	189	114	71	66
	Comb. N	26	12	10	5	92	48	30	26
Weight of nodules in % of total dry matter.	Free N ..	2·75	1·63	1·70	1·32	1·73	1·36	1·13	1·08
	Comb. N	0·57	0·66	0·29	0·38	0·54	0·37	0·40	0·27

The growth with combined nitrogen is at first somewhat better than with free nitrogen, but the difference disappears at the second harvest, and the uptake of nitrogen is only at the first harvest significantly lower from the acid sand, in spite of strong increase in acidity during the growth. In a few of these pots all the added nitrogen was used up and some extra nitrogen fixed, but as in Experiment No. 3, the gain per gm. nodule is very low (320–770 mgm.) in comparison with the figures in the free-nitrogen series. The numbers of nodules are greatly depressed by combined nitrogen in acid but less so in alkaline sand; the pH-values of the acid sand, however, are considerably lower in the combined-nitrogen than in the free-nitrogen series, and the decrease in nodule numbers may be as much due to the higher acidity as to the nitrogen *per se*. The decrease in numbers of nodules per gm. dry root and in the proportional weight of the nodules in the presence of combined nitrogen is again very marked.

Some determinations of residual ammonia and nitrate in the sand (mixed from replicate pots) were made in order to detect whether significant quantities of mineral nitrogen disappear otherwise than through uptake by the plants. The following approximate balance-sheet of nitrogen was found:

	Acid Sand, Days.			Alkaline Sand, Days.		
	74	88	102	74	88	102
Mgm. mineral N added per pot ..	240·0	300·0	360·0	240·0	300·0	360·0
Do. formed in unplanted sand ..	6·3	11·7	17·1	8·7	10·7	12·6
Sum	246·3	311·7	377·1	248·7	310·7	372·6
Do. found in sand after harvest ..	30·0	24·5	18·3	21·3	(0)	11·4
Disappeared from sand	216·3	287·2	358·8	227·4	310·7	361·2
Recovered in plants (total less seed-N)	223·3	271·2	357·1	251·3	320·9	376·9

Except in alkaline sand after 74 days the nitrogen contents of the plants correspond closely to the estimated amounts of disappeared mineral nitrogen, and there is no indication that significant proportions of the added nitrogen have been consumed by other processes such as denitrification or synthesis of microbial protoplasm in the sand or the rhizospheres.

Main Series of Experiments with Subterranean Clover.

These experiments were conducted as parallels to the experiments with lucerne, with the same nutrient treatments but different periods of growth and sometimes different sowing date.

Experiment No. 1 (cf. lucerne experiment No. 1, Table 3).—Clover was sown on 8th March, 1944, eight plants per pot, and harvested after 62, 92 and 125 days. The results are shown in Table 8. The sand without calcium carbonate became strongly acid during growth, and the final net gain of nitrogen appears lower than at neutral reaction, but wide variation between the replicates renders the difference non-significant. The numbers of nodules and the gains of nitrogen per gm. dry nodule are the same at both reactions, except that the numbers appear slightly higher after 62 days in neutral sand. The reaction showed a conspicuous effect on the appearance of the root nodules both in this and other experiments with subterranean clover; in acid sand the nodules were typically of a grapeseed-like shape and of more uniform size and distribution than in alkaline sand, where generally a limited number of big lobate nodules were found clustered round the top of the main root, while many small nodules were scattered over the rest of the root system.

Experiment No. 2 (cf. lucerne experiment No. 2, Table 4).—Clover was sown on 4th August, 1944, eight plants per pot, and harvested after 73, 94 and 115 days. As seen from Table 9, the growth in this sand has been strongly inhibited by calcium carbonate. Although the reaction is only moderately alkaline, the final net gain of nitrogen is little more than one-half of the gain in acid sand where vigorous nitrogen fixation has, as in Table 2, taken place during the last period at pH 4·2–4·8. The gains per gm. dry nodule are not, on the other hand, influenced by the wide difference in reaction. The actual numbers of nodules are lower in alkaline sand, except perhaps at the first harvest, but calculation of the numbers per gm. dry root show both in this and the previous experiment little effect of the reaction, again excepting the first stage of growth:—

	Experiment No. 1 (Table 8).			Experiment No. 2 (Table 9).		
Days	62	90	125	73	94	115
Nodules per gm. root :						
In acid sand	321	353	265	163	191	212
In alkaline sand	530	368	193	221	229	211

It thus appears that the infective power of *Rhizobium trifolii* towards *Trifolium subterraneum* is not lower at pH 4·7–5·0 than at pH 7·0–7·6, a result which agrees with previous observations in agar culture (Jensen, 1943). The lower numbers of nodules in the second experiment may be due to the higher content of metabolizable nitrogen in the hill sand.

Experiment No. 3 (cf. lucerne experiment No. 3, Table 5).—Sowing took place on 25th March, 1945; eight plants per pot were harvested after 75, 96, 116 and 130 days. The early growth was slow, and the combined-nitrogen pots were therefore given only two doses of ammonium sulphate, so that each pot received 240 mgm. nitrogen.

TABLE 8.

Nitrogen Fixation by Subterranean Clover, Experiment No. 1 (8/3/44--11/7/44).

Treatment.	Days.	pH of Sand.	Dry Matter, gm.			% N in Dry Matter.			Nodules per Plant, Mean and S.E.
			Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.	
-CaCO₃, Initial pH, 5·7	62	4·8-4·9	0·66	0·066	0·033	2·82	0·54	7·42	30·8±1·87
	90	4·9-5·0	1·17	0·18	0·069	3·34	2·19	7·55	63·5±2·95
	125	4·8-5·0	3·14	0·64	0·186	3·59	2·67	10·07	168·5±9·69
+CaCO₃, Initial pH, 6·8	62	6·9-7·2	0·61	0·081	0·023	3·38	0·42	7·68	42·9±3·77
	90	7·0-7·2	1·49	0·21	0·071	2·76	2·52	8·02	77·3±7·43
	125	7·1-7·2	4·69	0·93	0·197	3·43	2·21	8·47	179·9±15·1

Summary :

Days.	Total N in Plants, mgm.		Neg Gain of N, mgm.			Gain of N, mgm. per gm. Dry Nodule-substance.		
	-CaCO₃.	+CaCO₃.	-CaCO₃.	+CaCO₃.	Significance of Difference.	-CaCO₃.	+CaCO₃.	Significance of Difference.
62	21·5	22·9	16·9	12·0	...	519	528	—
90	48·2	51·9	36·8	37·7	...	530	532	—
125	148·6	197·9	136·2	186·1	—	732	944	—

TABLE 9.

Nitrogen Fixation by Subterranean Clover in Hill Sand, Experiment No. 2 (4/8/44-27/11/44).

Treatment.	Days.	pH of Sand.	Dry Matter, gm.			% N in Dry Matter.			Nodules per Plant, Mean and S.E.
			Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.	
-CaCO₃, Initial pH, 5·3-5·4	73	5·1-5·6	1·60	0·36	0·063	2·78	2·35	6·46	58·8±6·99
	94	4·7-4·8	3·53	0·73	0·155	3·04	2·58	6·56	139·1±13·0
	115	4·2-4·8	5·46	0·70	0·137	3·00	2·17	5·48	167·4±13·2
+CaCO₃, Initial pH, 7·3-7·6	73	7·2-7·6	1·27	0·20	0·045	2·67	2·28	6·41	44·2±3·18
	94	7·4-7·5	1·97	0·31	0·080	2·82	2·05	7·10	71·1±6·31
	115	7·3-7·6	4·19	0·46	0·079	2·35	2·30	5·61	97·1+5·44

Summary :

Days.	Total N in Plants, mgm.		Net Gain of N, mgm.		Significance of Difference.	Gain of N, mgm. per gm. Dry Nodule-substance.		Significance of Difference.
	-CaCO₃.	+CaCO₃.	-CaCO₃.	+CaCO₃.		-CaCO₃.	+CaCO₃.	
73	57·0	40·9	28·4	14·7	..	440	419	—
94	128·5	74·0	103·6	43·3	—.	665	532	—
115	188·3	113·2	153·4	87·6	+++	1152	1108	—

The results in Table 10 show considerable decrease in acidity of the acid sand at the two first harvests of the free-nitrogen series. The differences in net gain of nitrogen are not significant, but the gains per gm. dry nodule show a certain irregularity, being higher at acid reaction after 130 days, but at alkaline reaction after 96 and 116 days, and the means of the four values at each reaction are almost identical (935 and 925 mgm.). Apart from the first harvest the numbers of nodules are consistently higher in the acid sand, and this is further accentuated when the numbers are expressed on the basis of dry root weight. Apparently a reaction of pH 5·6–6·0 is very favourable for root infection; this reaction also appears optimal for growth of *Rhizobium trifolii* in pure culture (Snieszko, 1928; Jensen, 1942).

The combined-nitrogen series shows only slightly higher yields of dry matter and nitrogen than the free-nitrogen series. The total yields of nitrogen are not significantly different except at the first harvest, when the acid sand has become almost neutralized by the sodium nitrate. After 130 days all added nitrogen is used up and small extra amounts fixed in some of the pots; these gains corresponded to only 120–190 mgm. per gm. dry nodule. The numbers of nodules in acid sand are not much different from those in the corresponding series with free nitrogen, but in acid sand the numbers are quite low, particularly at the two first harvests. On a basis of dry root weight the

TABLE 10.

Nitrogen Fixation and Uptake of Combined Nitrogen by Subterranean Clover, Experiment No. 3.

Treatment.	Days.	pH of Sand.	Dry Matter, gm.			% N in Dry Matter.			Nodules per Plant Mean and S.E.
			Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.	
Free N,	75	6·1–6·2	0·70	0·10	0·022	3·95	2·51	8·71	14·6 + 1·71
—CaCO₃.	96	5·9–6·0	1·59	0·25	0·069	3·09	2·27	7·57	38·5 ± 7·52
Initial pH,	116	5·6–5·7	3·45	0·70	0·186	3·01	2·25	8·32	103·5 + 19·6
4·9–5·0	130	4·9–5·0	6·27	1·02	0·176	3·27	2·63	6·59	90·0 + 15·3
Free N,	75	7·2–7·3	0·88	0·16	0·035	3·20	2·22	8·34	14·9 + 2·61
+CaCO₃.	96	7·3–7·5	1·45	0·22	0·048	2·95	2·16	8·78	18·1 + 3·30
Initial pH,	116	7·3–7·4	3·45	0·59	0·138	3·63	2·22	7·90	40·6 + 9·69
6·8–6·9	130	7·2–7·3	6·23	1·28	0·224	2·88	1·09	6·53	61·4 + 10·9
Comb. N,	75	6·3–6·9	1·21	0·21	0·007	3·64	2·93	9·70	22·8 + 6·54
—CaCO₃.	96	6·4–6·5	1·96	0·33	0·014	3·33	2·57	9·65	40·5 + 11·6
Initial pH,	116	5·6–5·8	5·12	1·00	0·114	2·96	2·40	7·55	96·9 + 15·6
4·9–5·0	130	4·8–5·3	6·75	1·50	0·135	2·93	2·71	6·56	111·5 + 22·1
Comb. N,	75	7·0–7·2	0·64	0·10	0·003	4·21	2·67	...	7·2 + 1·24
+CaCO₃.	96	7·1 7·2	1·47	0·21	0·004	3·36	2·61	7·98	8·7 + 1·55
Initial pH,	116	7·3	4·17	0·93	0·043	3·15	2·45	7·09	42·5 + 10·4
6·8–6·9	130	7·2	7·19	1·63	0·113	2·93	2·38	7·47	58·7 + 14·4

Summary : Free-nitrogen series.

Days.	Total N in Plants, mgm.		Net Gain of N, mgm.		Significance of Difference.	Gain of N, mgm. per gm. Dry Nodule-substance.		Significance of Difference.
	—CaCO₃.	+CaCO₃.	—CaCO₃.	+CaCO₃.		—CaCO₃.	+CaCO₃.	
75	32·2	34·1	24·1	25·0	—	1019	852	...
96	60·7	51·8	51·6	43·9	...	735	904	+
116	134·8	149·4	126·2	142·0	—	682	1050	+ +
130	240·0	208·2	230·3	201·9	—	1304	803	+ +

Summary : Combined-nitrogen series.

Days.	Total N in Plants, mgm.		Significance of Difference.	Net Gain of N, mgm.		
	−CaCO₃.	+CaCO₃.		−CaCO₃.	+CaCO₃.	
75	50·4	29·8	+	(0)	(0)	Gain of nitrogen after 130 days
96	74·7	56·9	−	(0)	(0)	in one pot −CaCO₃ and
116	182·9	156·8	−	(0)	(0)	in two +CaCO₃.
130	248·9	252·4	−	(18·9)	(25·1)	

Relative Numbers and Weights of Nodules.		−CaCO₃, after Days.				+CaCO₃, after Days.			
		75	96	116	130	75	96	116	130
Number of nodules per gm. dry root.	Free N ..	1424	1239	1196	716	724	650	508	375
	Comb. N ..	844	1224	736	608	591	331	368	270
Weight of nodules in % of total dry matter.	Free N ..	2·71	3·40	4·25	2·35	3·22	2·81	3·27	2·92
	Comb. N ..	0·49	0·60	1·73	1·59	0·41	0·27	0·76	1·26

numbers of nodules are greatly diminished by alkaline reaction, and much less so by the provision of combined nitrogen. The proportional weight of the nodules is on the other hand not markedly influenced by the reaction, but is greatly depressed by combined nitrogen; it is noteworthy that the weight increases towards the end of the growth period when the sand has been exhausted of combined nitrogen and fixation begins to take place.

Experiment No. 4 (cf. lucerne experiment No. 4, Table 6).—Clover was sown on 1st August, 1945; six plants were left per pot and harvested after 63, 82, 96 and 110 days. The combined-nitrogen pots received at first 2 × 12 and later 2 × 24 mgm. nitrogen as ammonium nitrate per week, starting one week after sowing, so that the total doses at the four harvests amounted to 180, 276, 372 and 468 mgm. per pot. Growth was more vigorous in this than in any other experiment. Table 11 gives the results.

The acid sand in the free-nitrogen series shows rapidly increasing acidity. The net gains of nitrogen are all significantly lower than in the alkaline sand, but very strong fixation still takes place between the 82nd and 96th day, during which interval the pH-level falls from 5·0–5·2 to 4·3–4·7. The results of the final harvest are of limited significance because the growth increased very little during the last stage, and the roots showed signs of beginning decay at both acid and alkaline reaction.

The gain of nitrogen per gm. dry nodule is on the other hand at no stage significantly influenced by the reaction, but the figures are lower and the proportional weights of the nodules higher than in any other experiment. The numbers of nodules are, except at the first harvest, two to three times as high in acid as in alkaline sand, and the differences become even more pronounced when expressed in terms of nodules per gm. dry root. Results like these illustrate particularly well how little correlation there is between the actual gain of nitrogen and the number of nodules responsible for it.

The growth in the combined-nitrogen series, especially in the early stages, is even more vigorous than with free nitrogen, which suggests that favourable light and temperature conditions have given rise to a rate of photosynthesis too high for optimum nitrogen fixation (cf. Wilson, 1940); possibly the unusually high proportional weight of

the nodule-fraction might be explained through this. The acid sand shows pH-values as low as in the free-nitrogen series, but the nitrogen content of the plants is at no stage significantly lower, but rather higher, than in the alkaline sand. After 96 days the added nitrogen was used up in all the acid and one of the alkaline pots, and small amounts of nitrogen were fixed (110–210 mgm. per gm. dry nodule, against 550–600 mgm. in the free-nitrogen series after 96 days); this is accompanied by a notable increase in the proportional weight of the nodules, as in the previous experiment (Table 10). During the final stage very little nitrogen was taken up from the alkaline and none from the acid sand; the apparent decrease in nitrogen content is not significant. The roots showed obvious signs of decay after 110 days, and some nodules were probably lost. The actual numbers of nodules, in comparison with the free-nitrogen series, are only depressed by combined nitrogen at the two last harvests in acid sand; the numbers per gm. dry root show a large decrease at all stages and both reactions, and the same applies to the proportional weight of the nodule-fraction.

TABLE 11.

Nitrogen Fixation and Uptake of Combined Nitrogen by Subterranean Clover, Experiment No. 4 (1/8/45–19/11/45).

Treatment.	Days.	pH of Sand.	Dry Matter, gm.			% N in Dry Matter.			Nodules per Plant, Mean and S.E.
			Tops.	Roots.	Nodules.	Tops.	Roots.	Nodules.	
Free N,	63	5·1–5·2	1·06	0·28	0·095	2·87	2·15	7·33	55·6 ± 3·73
–CaCO₃.	82	5·0–5·2	2·30	0·58	0·156	2·88	2·33	6·73	123·3 ± 7·76
Initial pH,	96	4·3–4·7	5·82	1·55	0·323	2·53	2·36	6·24	255·8 ± 16·5
5·8	110	4·2–4·4	6·82	1·73	0·375	2·47	2·13	5·42	241·4 ± 14·2
Free N,	63	7·1–7·4	1·47	0·46	0·135	2·88	2·10	7·90	56·2 ± 2·61
+CaCO₃.	82	7·3–7·5	3·76	1·01	0·228	2·80	2·13	6·93	66·1 ± 3·89
Initial pH,	96	7·1–7·2	8·71	2·08	0·476	2·44	2·19	6·52	80·5 ± 3·18
7·0	110	7·5–7·6	10·74	2·16	0·487	2·40	2·03	5·48	101·8 ± 8·43
Comb. N,	63	5·1–5·2	3·70	1·24	0·051	2·81	2·74	6·88	117·8 ± 10·4
–CaCO₃.	82	5·0–5·9	7·04	2·06	0·150	2·74	2·55	6·98	120·2 ± 8·38
Initial pH,	96	4·3–4·7	10·62	3·75	0·241	2·73	2·70	6·19	131·9 ± 7·75
5·8	110	4·2–4·4	11·62	3·51	0·163	2·52	2·44	5·62	115·9 ± 10·8
Comb. N,	63	7·5–7·6	2·80	0·96	0·020	3·17	2·82	6·03	75·6 ± 9·46
+CaCO₃.	82	7·4–7·7	5·80	1·96	0·052	2·75	2·62	6·48	73·3 ± 5·57
Initial pH,	96	7·3–7·5	10·18	3·35	0·131	2·67	2·63	7·18	72·8 ± 3·21
7·0	110	7·2–7·5	12·81	3·88	0·195	2·42	2·13	6·00	93·0 ± 7·65

Summary: Free-nitrogen series.

Days.	N in Plants, mgm.		Net Gain of N, mgm.		Significance of Difference.	Gain of N, mgm. per gm. Dry Nodule-substance.		Significance of Difference.
	–CaCO₃.	+CaCO₃.	–CaCO₃.	+CaCO₃.		–CaCO₃.	+CaCO₃.	
63	43·6	62·7	34·2	56·0	+	361	414	–
82	90·3	142·5	80·9	135·8	+ + +	518	597	–
96	205·1	289·0	196·1	281·7	+ + +	552	602	–
110	226·0	328·3	216·9	320·4	+ + +	587	682	–

Summary : Combined-nitrogen series.

Days.	N in Plants, mgm.		Significance of Difference.	Net Gain of N, mgm.		
	−CaCO₃.	+CaCO₃.		−CaCO₃.	+CaCO₃.	
63	146·4	116·8	—			Gain after 96 days in alkaline
82	257·2	214·4	+ +			sand in one pot only.
96	410·3	369·2	—	28·0	(44·4)	
110	386·9	404·3	—			

Relative Numbers and Weights of Nodules.		−CaCO₃, after Days.				+CaCO₃, after Days.			
		63	82	96	110	63	82	96	110
Nodules, number per gm. dry root.	Free N ..	1191	1263	1011	837	744	398	232	280
	Comb. N	567	342	181	191	436	224	133	155
Weight of nodules in % of total dry matter.	Free N ..	6·65	5·14	4·61	4·15	6·63	4·58	4·23	3·64
	Comb. N	0·90	1·23	1·65	1·03	0·51	0·66	0·93	1·15

THE NITROGEN-FIXING EFFICIENCY OF ROOT NODULE TISSUE IN LUCERNE AND SUBTERRANEAN CLOVER.

From the data of the preceding experiments with lucerne and clover grown with free nitrogen we may now calculate the rates of nitrogen fixation by the nodule tissue at successive stages of growth, by the formula of Bond (1936) :

$$E = \frac{I}{t \times (w_1 + w_2)/2}$$

where E represents the efficiency of the nodules as fixation of nitrogen in mgm. per gm. dry nodule-substance per day, I the increase in net gain of nitrogen per pot in t days, and w_1 and w_2 the dry weight of the nodules at the beginning and the end of the period.

The figures for lucerne are shown in Table 12, together with the ratios between the amount of nitrogen fixed per day and the mean nitrogen content of the nodules at the beginning and the end of the period. These figures thus express the efficiency of fixation on the basis of nodule nitrogen (E_n) instead of total dry matter ($E_{d.m.}$). The table also contains the rates of transfer of fixed nitrogen from the nodules to the rest of the plant; this is expressed as net gain of top and root nitrogen in per cent. of total net gain, it being assumed that all nitrogen in the nodules results from fixation and not from the small uptake of combined nitrogen.

During the first period of growth the efficiency cannot be determined accurately because we do not know how many days elapse before the nodules begin to function (probably some 10 to 20 days, to judge from the appearance of the first true leaves, which coincides approximately with the beginning of fixation [Fred et al., 1932]); these figures thus represent minimum values. The subsequent rates of fixation vary between 11 and 103 mgm. nitrogen per gm. dry nodule per day. Only in three instances (Experiment No. 2 at pH 4·5–4·8 and Experiment No. 3 at pH 4·9–5·7) is there a real indication of reduced nodular efficiency at acid reaction, and in Experiment No. 3 the decline in the 76–91 days period even occurs after a period of exceptionally high efficiency and may thus not be related exclusively to the reaction. The mean values of $E_{d.m.}$ at acid and alkaline reaction are not significantly different and similar to the (somewhat too high)

value of 57 mgm. found by Wozak (1929) under field conditions. The values of E_n show that the daily yield of the fixation process often approaches the nitrogen content of the nodules and sometimes exceeds it by as much as one-third. On the average the nodules fix 73 to 80% of their own nitrogen content daily, and at least 89 and mostly 95–96% of this is even in the early stages transferred to the rest of the plant. This rate of transfer is considerably higher than in soy beans and cowpeas, where 20% or more of the fixed nitrogen may be retained by young nodules, as shown by Whiting

TABLE 12.
Nitrogen-fixing Efficiency of Lucerne Root Nodules.

Experiment Number.	Days.	Acid Sand.				Alkaline Sand.			
		pH.	$E_{d.m.}$	E_n.	Trans. %.	pH.	$E_{d.m.}$	E_n.	Trans. %.
1. (Table 3.)	0	5·7	(>53)	(>0·71)	96	6·7	(>44)	(>0·56)	95
	64	5·0–5·7	60	0·85	95	6·9–7·0	68	1·11	96
	92	5·1–5·5	52	0·63	94	7·1–7·2	57	0·67	94
	120	4·6–4·8				7·0–7·1			
2. (Table 4.)	0	5·1	(nil)	(nil)		7·2	(>23)	(>0·30)	89
	60	4·8–5·0	88	1·18	94	7·1–7·2	77	0·94	96
	85	4·6–4·8	30	0·42	95	7·0–7·4	86	1·09	(100)
	100	4·5–4·6				7·2–7·5			
3. (Table 5.)	0	5·4–5·5	(>39)	(>0·58)	94	6·8–7·0	(>47)	(>0·70)	95
	56	6·0–6·2	103	1·36	96	7·3–7·4	62	0·72	94
	76	5·1–5·7	20	0·28	89	7·6–7·8	60	0·83	97
	91	5·1–5·4	11	0·15	(103)	7·2–7·3	41	0·50	98
	105	4·9–5·4				7·2–7·3			
4. (Table 6.)	35	6·1–6·2	43	0·65	91	7·0	42	0·70	92
	68	5·8–6·2	49	0·73	97	7·2–7·5	55	0·80	97
	88	5·4–5·6	44	0·67	98	7·2–7·5	38	0·55	94
	102	5·3–5·6				7·3–7·4			
5. (Table 7.)	0	5·4–5·7	(>34)	(>0·55)	94	7·1–7·3	(>57)	(>0·82)	96
	59	5·4–5·9	90	1·30	97	7·6–7·7	80	1·18	98
	74	5·3–5·6	43	0·59	95	7·0–7·3	46	0·60	96
	88	5·1–5·6	60	0·80	97	7·3–7·5	50	0·67	99
	102	6·0–6·1				7·4–7·6			
Mean			53	0·73	95		59	0·80	96

$E_{d.m.}$ = mgm. nitrogen fixed per day per gm. dry nodule-matter.
E_n = same per mgm. nodule-nitrogen.

(1915), Bond (1936), and Wilson and Umbreit (1937). In one or two instances the nitrogen content of the nodules remains stationary or decreases during the last period, with the result that the transfer equals or exceeds the fixation.

The corresponding figures for subterranean clover are seen in Table 13. Apart from the somewhat abnormal case represented by the final stage of Experiment No. 4, when growth had almost ceased, the average rate of nitrogen fixation by clover nodule tissue appears to be somewhat less than one-half of that of lucerne. The values of $E_{d.m.}$ range from 14 to 41 at acid and 22 to 53 at alkaline reaction, and the means are not significantly different. The E_n-values show, if we again disregard the last stage of Experiment No. 4, that the nodules fix from about one-sixth (Experiment 1, 62–90 days, pH 4·8–5·0) to two-thirds (Experiment No. 3, 96–116 days, pH 7·3–7·5), and on the average one-third, of their own nitrogen content per day. There is again no significant difference between the two ranges of reaction. Owing to the higher proportional weight

TABLE 13.

Nitrogen-fixing Efficiency of Subterranean Clover Root Nodules.

Experiment Number.	Days.	Acid Sand.				Alkaline Sand.			
		pH.	$E_{d.m.}$	E_n.	Trans. %.	pH.	$E_{d.m.}$	E_n.	Transf. %.
1. (Table 8.)	0	5·7				6·7			
			(>17)	(>0·22)	85		(>0·17)	(>0·21)	85
	62	4·8–4·9				6·9–7·1			
			14	0·18	86		20	0·25	85
	90	4·9–5·0				7·0–7·2			
			22	0·24	86		32	0·37	93
	125	4·8–5·0				7·1–7·2			
2. (Table 9.)	0	5·3–5·4				7·1–7·3			
			(>12)	(>0·19)	86		(>9)	(>0·18)	85
	73	5·1–5·6				7·2–7·4			
			33	0·50	92		22	0·35	88
	94	4·7–4·8				7·4–7·5			
			16	0·27	(105)		27	0·43	(103)
	115	4·2–4·8				7·3–7·6			
3. (Table 10.)	0	4·9–5·0				6·8–6·9			
			(>20)	(>0·33)	92		(>19)	(>0·23)	88
	75	6·1–6·2				7·2–7·4			
			30	0·37	84		22	0·25	93
	96	5·9–6·0				7·3–7·5			
			29	0·36	86		53	0·65	93
	116	5·6–5·7				7·3–7·4			
			41	0·55	(104)		23	0·34	92
	130	4·9–5·0				7·2–7·3			
4. (Table 11.)	0	5·8				7·0			
			(>11)	(>0·16)	80		(>13)	(>0·17)	81
	63	5·1–5·2				7·1–7·4			
			20	0·28	92		23	0·32	94
	82	5·0–5·2				7·3–7·5			
			34	0·50	90		29	0·44	90
	96	4·3–4·7				7·1–7·4			
			4	0·07	(105)		6	0·10	89
	110	4·2–4·4				7·5–7·6			
Mean ..			23	0·33	91		26	0·35	90

$E_{d.m.}$ = mgm. nitrogen fixed per day per gm. dry nodule-matter.
E_n = same per mgm. nodule-nitrogen.

and nitrogen content of the clover nodules, the rate of nitrogen transfer is somewhat lower than in lucerne—mostly 85 to 94%, but sometimes exceeding 100% in the later stages when the nitrogen content of the nodules begins to decrease. As a whole the figures for nodule efficiency and nitrogen transfer in subterranean clover are comparable to those found in young soy bean plants by Bond (1936) and Wilson (1940). A somewhat higher efficiency value (55 mgm.) was calculated by Wozak (1929) in red clover under field conditions, but this figure may be regarded as somewhat too high, and also the figures in Table 1 suggest a higher efficiency of nodules in white clover than in subterranean clover. On the other hand the efficiency of red clover nodules in the experiments of Chen and Thornton (1940) appears remarkably low, as mentioned in the introduction, and it might be questioned whether the equal efficiency of "effective" and "ineffective" nodules in equal time and tissue volume, which Chen and Thornton observed, would also exist under conditions permitting a generally higher level of efficiency (cf. Boyes and Bond, 1942, on soy beans).

EFFECT OF MOLYBDENUM ON THE EFFICIENCY OF ROOT NODULE TISSUE.

A supplementary experiment was performed in order to test the possible effect of molybdenum and the influence of reaction on the availability of the reserves of this element in the sand. The following nutrients were given: KH_2PO_4, 0·4 gm., $CaCl_2$, 0·4 gm., $MgSO_4$, 0·2 gm., $NaCl$, 0·2 gm., $FeCl_3$, 0·04 gm., minor salts (with and without Na_2MoO_4), 1·2 mgm., and 0·1% $CaCO_3$ in the alkaline sand. Each treatment included four replicate pots. Lucerne, six plants per pot, was sown on 31st May, 1946, and harvested after 101 days, and subterranean clover (seven plants) on 30th May, 1946, and harvested after 110 days. The results are shown in Table 14.

The net gains of nitrogen by lucerne are not significantly different, but the gains per gm. dry nodule show a clear effect of both reaction and molybdenum. The highest weight of the nodule-fraction, both absolutely and proportionally, and the lowest gain of nitrogen per gm. dry nodule, are found in acid sand without molybdenum. Addition of molybdenum results in an increase in gain per gm. nodule, significant at the 5% point; a further increase is produced by calcium carbonate, but molybdenum in addition to this is without effect. Determinations of molybdenum by Marmoy's thiocyanate method (Piper, 1942) show approximately 25 p.p.m. Mo in nodule substance from the treatment "+ $CaCO_3$ – Mo", which has a higher nitrogen-fixing efficiency than nodule substance from the treatment "– $CaCO_3$ + Mo" with its 50% higher molybdenum content. It thus appears that in this sand the acid reaction has reduced the efficiency of the nodules *partly* by limiting the uptake of molybdenum, but also in other ways, and that the molybdenum concentration of lucerne nodule tissue necessary for maximum efficiency lies somewhere between 10 and 25 parts per million.

(It should be noted that these figures are probably a little too high. The analyses were made before it was realized that the presence of iron tends to exaggerate the molybdenum figures, as shown by Dick and Bingley (1946). Sufficient material was not available for renewed molybdenum determinations, but analyses of some other materials suggested that the figures should be reduced by some 10 to 20%.)

The net gains of nitrogen by clover are likewise unaffected by either reaction or molybdenum supply, and the gain per gm. dry nodule is lowest in acid sand without molybdenum; this is increased very significantly (beyond the 1% point) by addition of either molybdenum or calcium carbonate, but the reaction *per se* appears to have no effect, inasmuch as the gain per gm. nodule in acid sand with molybdenum is as high as at alkaline reaction. The molybdenum determinations, in which precautions were taken against the effect of iron, show that a content of about 4 p.p.m. Mo is insufficient for maximum efficiency of the nodules, but no further effect results from raising the content above 7–8 p.p.m. Mo. The effect of calcium carbonate on subterranean clover in the absence of added molybdenum thus seems to consist chiefly in rendering the molybdenum of the sand medium available to the plants (cf. Anderson and Oertel, 1946), while in lucerne it also has other effects. The question naturally arises whether this

lower molybdenum requirement of the clover nodule tissue has a causal connection with its generally lower nitrogen-fixing efficiency and its lesser sensitivity to acid reaction in comparison with lucerne.

TABLE 14.

Influence of Hydrogen Ion Concentration and Molybdenum on Nitrogen Fixation by Lucerne and Subterranean Clover.

		Lucerne (31/5/46–9/9/46).				Clover (30/5/46–17/9/46).			
		−CaCO₃.		+CaCO₃.		−CaCO₃.		+CaCO₃.	
		− Mo.	+ Mo.	− Mo.	+ Mo.	− Mo.	+ Mo.	− Mo.	+ Mo.
pH of sand, initial		5·7	5·7	7·5	7·5	5·7	5·7	7·5	7·5
,, ,, ,, final		4·7–4·9	4·6–4·9	6·8–7·0	6·6–6·9	4·7–4·9	4·8–5·0	7·0–7·4	7·4–7·5
Dry matter, gm. per	Tops	4·14	4·24	4·71	4·61	6·61	6·83	7·45	7·72
pot, mean.	Roots	3·21	3·49	3·17	3·23	1·99	1·85	1·93	2·02
	Nodules	0·219	0·180	0·124	0·121	0·367	0·287	0·302	0·288
Percentage of N in	Tops	3·51	3·76	3·56	3·53	3·07	3·09	2·96	3·05
dry matter.	Roots	2·19	2·56	2·41	2·33	2·52	2·66	2·33	2·15
	Nodules	6·45	7·20	7·96	7·90	6·98	6·95	6·81	6·84
Molybdenum in dry	Tops	0·4	7·7	1·1	28·1	0·6	13·4	0·9	33·2
matter, p.p.m.	Roots	1·0	8·1	1·4	23·0	1·1	6·7	1·0	12·8
	Nodules	9·6	37·5	24·8	73·7	4·4	7·1	7·4	15·9
Total N in plants, mgm.		229·9	261·8	253·7	247·4	278·4	280·0	286·0	298·8
Net gain of N, mgm.		222·8	254·7	244·5	238·2	268·1	269·7	273·6	286·4
Do. per gm. dry nodule-substance		1040	1496	1974	1974	735	946	906	991
Total Mo in plants, γ		7·0		12·3		7·8		10·9	
Mgm. N per γ Mo		32·8		20·6		35·7		26·2	
Nodules per plant.	Mean	32·4	22·0	46·8	47·1	424	292	314	320
	S.E.	±3·98	±1·01	±2·76	±4·18	±34·0	±18·8	±23·7	±21·9

	Significant difference at P.			Significant difference at P.		
	0·05	0·02	0·01	0·05	0·02	0·01
Net gain of N	39·6	48·7	55·5	39·4	48·5	55·2
Do. per gm. dry nodule-substance	401	483	562	108	133	151

The counts of nodules in both plants show that in acid sand the numbers are significantly lowered by the addition of molybdenum, while the pH-values show no corresponding difference. In the presence of calcium carbonate, which has rendered the molybdenum in the sand more available, the further addition of molybdenum has no such effect on the numbers of nodules. The phenomenon of reduction in numbers of nodules by supply of molybdenum to soil deficient in this element has already been observed by Anderson and Thomas (1946), who also conclude that the effect of molybdenum on legumes consists in stimulation of the nitrogen-fixing activity of the nodule tissue. This contention, although based only on numbers and not on mass of nodules, is fully confirmed by the present results which emphasize that a sufficient supply of available molybdenum is an important factor to be considered in experiments on the effect of reaction on symbiotic nitrogen fixation.

Several earlier experiments on this problem seem to acquire a new aspect in the light of these findings, as well as those of Oertel *et al.* (1946), which strikingly illustrate the effect of molybdenum in widening the pH-limits for growth of subterranean clover. The reduction in the efficiency of subterranean clover nodules in acid sand and soil

observed previously (Jensen, 1943, 1944) might well be due simply to inhibited uptake of molybdenum. The results with lucerne seem also to need reinterpretation. It was observed (Jensen, 1946) that not only the efficiency of the nodules (gain of nitrogen per gm. dry matter), but also the actual yields of nitrogen, are lowered at a content of only 2·7 p.p.m. Mo in the nodule substance, a result which agrees with the fact that the efficiency, but not necessarily the actual yield, begins to suffer at a limit close to or somewhat above 10 p.p.m. Mo in lucerne nodule substance. This may explain why earlier experiments (Jensen, 1943, 1944; cf. also Olsen, 1925) showed that lucerne grown in soil of pH about 5 fixed only about half as much nitrogen as at pH 7·0–7·3; the sand-soil-mixture used for the main experiments with lucerne (1943, Table 8; 1944, Table 2) was the same as used in another experiment (Jensen and Betty, 1943), where nodules of lucerne were found to contain only 3·2 p.p.m. Mo at pH 4·9–5·4 against 10 p.p.m. at pH 7·5–8·0. Such a difference in the molybdenum content would be quite likely to have a considerable effect on the gain of nitrogen, apart from the difference in reaction.

The records of several other investigations on the growth of legumes in soil, sand, or water culture at different reaction, discussed by Fred *et al.* (1932) and Wilson (1940), seem also to admit the possibility of molybdenum deficiency at the lower pH-ranges. In sand culture experiments with soy beans, Hopkins (1935) found that pH-values below 6 were unfavourable for growth with free nitrogen, although not with nitrate, and gave rise to pathological symptoms (chlorotic spots on the leaves) which were suggestive of molybdenum deficiency and disappeared when the reaction was corrected. Alway and Nesom (1927) observed in field trials with lucerne on acid soil (pH 5·0–5·7) a far greater benefit from soil transfer than from pure culture inocula which were effective only when lime was applied. The authors suggest as one possible explanation the presence in the inoculating soil of small amounts of some chemical compound beneficial to the bacteria. The possibility of this active element being molybdenum suggests itself.

GENERAL CONCLUSIONS.

If we try to form a general picture from the preceding experiments, we find first that the reaction of the medium, as in previous experiments (Jensen, 1943), shows different effects on the *formation* and on the *development* and *activity* of the root nodules. In lucerne the numbers of nodules decrease at acid reaction, particularly in the pH-interval from about 6 to 5, but in subterranean clover the numbers are highest at pH 4·5–5·5 and tend to decrease at neutral or faintly alkaline reaction. This may be regarded as showing the effect of reaction on the ability of the nodule bacteria, existing outside the plants, to invade the roots and form nodules. *Rhizobium trifolii* thus appears far more acid-tolerant than *Rhizobium meliloti*, and this agrees to some extent with the behaviour of these bacteria *in vitro* (Jensen, 1942). However, the acid-tolerance in sand medium appears considerably greater; lucerne forms nodules at pH 5 and less (cf. Olsen, 1925, who found sparse nodule formation in soil of pH 4·0–4·4), and a pH-range of 4·5–5·0 is unfavourable for survival of *Rhizobium trifolii* in soil (Bryan, 1923; Wilson, 1926, 1931) and prohibitive to growth in pure culture (Snieszko, 1928; Jensen, 1942), although not to nodule formation in agar medium (Jensen, 1942). Further investigations on this point are needed.

The mass of root nodule tissue is little affected by the reaction because, especially in lucerne, the smaller number of nodules in acid sand is compensated by increased size of individual nodules. The same applies to the nodular efficiency, expressed as gains of nitrogen per gm. dry matter, which in lucerne shows definite decreases only at pH 5 and less, and which in subterranean clover remains unaffected at pH 4·5–4·8 (adequate molybdenum supply presupposed). This comparative insensivity of the nitrogen fixation process to the reaction of the external medium must evidently be ascribed to the fact that once the nodule bacteria have gained entry into the plant, the external reaction can only influence their activities through its effect on the assimilation of mineral nutrients and on the internal reaction of the root and especially the nodule tissue. However, the intranodular reaction appears within wide limits

independent of that of the growth substrate (Jensen, 1943), and the present experiments with combined nitrogen, especially Tables 7 and 11, show no evidence of inhibited uptake of minerals, as growth was equally good at acid and alkaline reaction.

The lack of correlation between the numbers of root nodules and the resulting nitrogen fixation must be viewed on the background of the fact that a heavy inoculum of nodule bacteria was provided in all cases. A certain minimum number of nodules may be regarded as necessary for maximum fixation, since there would obviously be limits to the ability of the plant to compensate for the lower number of nodules by increased nodule size, and in a medium harbouring a sparse population of *Rhizobium* an unfavourable reaction might well prevent this number from being reached. A complete answer to the question of interrelation between the reaction of the medium, the number and the mass of nodules, and the efficiency of the nodule tissue could probably be obtained by growing the plants at several constant pH-levels (flowing nutrient solution) and periodically determining the intranodular pH as well as increases in dry matter and nitrogen. By altering the reaction of the medium during growth it should be possible to define the pH-limits at which not only the formation of new nodules but also the activity of those already formed is completely inhibited.

The provision of combined nitrogen in quantities similar to, or somewhat higher than, the amounts fixed in the free-nitrogen series has comparatively little influence on the actual numbers of nodules, but tends to lower the numbers in proportion to the weight of the roots. The average size of the nodules is greatly diminished, and the proportional weight of the nodule fraction is reduced to roughly one-fourth of its value in the free-nitrogen series, as shown by the following summary of the weight of nodules in percentage of total dry matter:

	Lucerne. (Tables 5–7.) %	Subterranean Clover. (Tables 10–11.) %
Free N	1·08–4·23	2·35–6·65
Combined N	0·26–1·16	0·27–1·73

At the same time the nitrogen fixation almost ceases although it may continue if the combined nitrogen is used up. The inhibitory effect of combined nitrogen on nitrogen fixation seems due to reduced development of nodule tissue, as found by Nicol and Thornton (1936), as well as to lower efficiency of the tissue formed, probably because the available carbohydrates are largely used for protein synthesis with the combined mineral nitrogen (cf. Wilson, 1940). There is no evidence that the total amount of root and nodule substance in proportion to the tops is decreased by combined nitrogen, as stated by Allison and Ludwig (1934).

The data on the nodule efficiency in Tables 12 and 13 may permit some tentative considerations on certain aspects of the mechanism of nitrogen fixation and transfer. Bond (1936) concluded from experiments with soy beans that the fixation is a kind of respiration process which results in a steady transfer of some 80–90% of the fixed nitrogen from the nodules to the rest of the plant. Wilson and Umbreit (1937), on the other hand, thought that the observations might equally well be explained on the basis of the views commonly held before, that transfer takes place through disintegration of the bacteria in the nodules by proteolytic enzymes of the host cells, autolysis, or a bacteriophage, and subsequent transport of the soluble nitrogenous digestion products.

The present experiments, particularly with lucerne, show a turnover of nodule-nitrogen considerably more rapid than in soy beans. If we assume with Bond (1941) that the bacterial tissue accounts for roughly one-half of the whole nodule, the values of $E_{d.m.}$ (Tables 12 and 13), which should properly refer to dry bacterial tissue, would be approximately doubled. The bulk of the nodule-nitrogen is in the bacterial tissue,

and the perifereal tissue may probably without grave error be assumed to have the
same gross chemical composition as the rest of the root substance (cf. Bond, 1941).
The analyses in the preceding tables show that in lucerne grown with free nitrogen the
ratio ($\%$ N in nodules)/($\%$ N in roots) varies between 2·77 and 6·14, with a mean value
of 3·35. The corresponding figures for clover, apart from two abnormal cases in Table 8,
62 days, are 2·33, 5·99, and 3·15. This indicates that on the average the perifereal tissue
contains 23–24 and the bacterial tissue 76–77%, or roughly three-fourths, of the total
nodule nitrogen. A calculation on this basis would raise the values of E_n in Tables 12
and 13 by one-third; the nitrogen content of the bacterial tissue in lucerne would then
on the average renew itself in about 24 hours, and in clover in somewhat more than
two days. However, the bacterial tissue consists of *Rhizobium*-cells ("bacteroids") and
host cells, of which the relative weights are not known, but the former have probably the
higher nitrogen content. We may perhaps assume that the bacteria contain two-thirds
of the bacterial-tissue nitrogen or one-half of the total nodule nitrogen; the E_n values
calculated on the basis of bacteria alone would then be doubled. Provided that the
bacteria and not the host cytoplasm are the site of nitrogen fixation, and that the
transferred nitrogen is derived from dead bacterial cells only, the average E_n values in
lucerne (Table 12) would imply a renewal of the whole bacterial nodule population every
15 or 16 hours, in extreme cases (Experiment No. 3, acid sand, 56–76 days) even every
9 hours. While such a rate of reproduction may be conceivable, it appears unlikely in
view of the generally low reproductive capacity of bacteroids taken from nodules (Fred
et al., 1932; Almon, 1933). The rate of nitrogen turnover would thus seem to fit better
with Bond's idea of transfer of a nitrogenous compound secreted by the bacteria during
active metabolism. This seems also supported by the fact that when nitrogenous root
secretion occurs, it takes the form of an apparent key-compound of the nitrogen fixation
process: aspartic acid or its derivative β-alanine (Virtanen, 1938), or, according to more
recent evidence (Virtanen et al., quoted by Wilson and Burris, 1947), a mixture of
glutamic acid, aspartic acid, and β-alanine.

It also seems entirely possible that the transferred nitrogen may originate from two
sources: excess of a key-compound of the nitrogen fixation process (glutamic acid?), and
digestion products of bacteroids dying during the life history of the nodule population.
The actual existence of the last process seems indicated by the fact that the total
nitrogen content of the nodule-fraction often decreases during the later stages of the
plant's life. Investigations on the almost untouched problem of the rise and fall of
the bacterial population in the nodules might contribute to assessing the relative
importance of these two processes. The present evidence would seem to favour the
"secretion" rather than the "digestion"-hypothesis.

SUMMARY.

Pot experiments with pasture legumes, mostly lucerne and subterranean clover,
were conducted in sand of acid and faintly alkaline reaction. The rate of nitrogen
fixation by the root nodule tissue was measured by determining the dry weight and
nitrogen content of the separate fractions of tops, roots and root nodules at successive
stages of growth.

Root nodules of lucerne fixed from 11 to 103 (average, 56) mgm. nitrogen per gm.
dry matter per day, or 0·15 to 1·36 times their own nitrogen content. Significant decreases
in nodule-efficiency at acid reaction were only observed in sand of pH near or below 5,
but fixation still took place at pH 4·5–4·8. The net gain of nitrogen per pot also as a rule
declined significantly only at pH about 5 or less. Generally 94 to 98% of the fixed
nitrogen was transferred from the nodules to the rest of the plant.

Nodules of subterranean clover showed a consistently lower rate of activity. Under
conditions of vigorous growth 14 to 53 mgm. nitrogen were fixed per day per gm. dry
matter, or 0·13 to 0·65 times the nodule nitrogen content. Mostly 80 to 94% of the fixed
nitrogen was transferred to the rest of the plant. The fixation per gm. dry nodule was
not significantly influenced by the reaction. The net gain per pot sometimes showed
decrease at pH about 5 and less, but nitrogen was still fixed in sand of pH 4·2–4·5.

The numbers of root nodules in lucerne decreased conspicuously in sand of pH about 5·5 and less. This decrease was associated with an increase in the size of individual nodules. Nodules of subterranean clover were, on the other hand, usually more numerous in acid than in alkaline sand, and the influence of the reaction on their size was less conspicuous than in lucerne. No correlation was found between the numbers of nodules and the resulting nitrogen fixation, which is determined by the aggregate mass rather than the numbers of nodules.

Combined nitrogen supplied as nitrate or ammonia in quantities comparable to the amounts of nitrogen fixed in the same time had relatively little effect on the numbers of nodules, but reduced their weight and nitrogen-fixing efficiency greatly. Both lucerne and subterranean clover grew nearly equally well at pH 4·5-5·0 and at pH 7·0-7·5 when given combined nitrogen.

A molybdenum content of lucerne nodules between approximately 10 and 25 p.p.m. dry substance appeared necessary for maximum nitrogen-fixing efficiency of the nodule-tissue. The results of earlier experiments suggest that the actual gain of nitrogen decreases when the nodule substance contains only 3 to 10 p.p.m. molybdenum. In nodules of subterranean clover a molybdenum content between 4 and 8 p.p.m. was required for full efficiency per gm. nodule, but the actual gain of nitrogen did not decrease when the nodules contained only 4 p.p.m. molybdenum.

ACKNOWLEDGEMENTS.

REFERENCES.

ALLISON, F. E., and LUDWIG, C. A., 1934.—The Cause of Decreased Nodule Formation on Legumes Supplied with Abundant Combined Nitrogen. *Soil Sci.*, 37: 431-443.

ALMON, L., 1933.—Concerning the Reproduction of Bacteroids. *Cent. Bakt.*, II, 87: 289-297.

ALWAY, F. J., and NESOM, G. H., 1927.—Inoculation of Alfalfa on Lime-deficient Sandy Soil. *Minn. Agric. Exp. Stat. Tech. Bull.* No. 46; 62 pp.

ANDERSON, A. J., and OERTEL, A. C., 1946.—Plant Responses to Molybdenum as a Fertilizer. 2. Factors Affecting the Response of Plants to Molybdenum. *Counc. Sci. Indus. Res.* (Melbourne), Bull. No. 198: 25-44.

————, and THOMAS, MARGARET P., 1946.—Plant Responses to Molybdenum as a Fertilizer. 1. Molybdenum and Symbiotic Nitrogen Fixation. Ibid., 198: 1-24.

BOND, G., 1936.—Quantitative Observations on the Fixation and Transfer of Nitrogen in the Soy Bean (etc.). *Ann. Bot.*, 50: 559-578.

————, 1941.—Symbiosis of Leguminous Plants and Nodule Bacteria. Ibid. (N.S.), 3: 313-337.

BOYES, J., and BOND, G., 1942.—The Effectiveness of Certain Strains of the Soya Bean Nodule Organism when Associated with Different Varieties of the Host Plant. *Ann. Appl. Biol.*, 29: 103-108.

BRYAN, O. C., 1923.—Effect of Acid Soil on Nodule-forming Bacteria. *Soil Sci.*, 15: 37-40.

CHEN, H. K., and THORNTON, H. G., 1940.—The Structure of "Ineffective" Nodules and its Influence on Nitrogen Fixation. *Proc. Roy. Soc. London* (B), 129: 208-229.

DICK, A. T., and BINGLEY, J. B., 1946.—Molybdenum-thiocyanate Complex. *Nature*, 158: 516. (Also *Aust. J. Exp. Biol.*, 25 (1947): 193-202.)

FISHER, R. A., 1946.—Statistical Methods for Research Workers. 10th ed., London.

FRED, E. B., BALDWIN, I. L., and McCOY, ELIZABETH, 1932.—Root Nodule Bacteria and Leguminous Plants. (Madison, Wis.)

GIÖBEL, G., 1926.—The Relation of the Soil Nitrogen to Nodule Development and Fixation of Nitrogen by Certain Legumes. *N.J. Agric. Exp. Stat. Bul.* No. 436: 125.

HOPKINS, E. W., 1935.—The Effect of Long and Short Day and Shading on Nodule Development and Composition of the Soybean. *Soil Sci.*, 39: 297-322.

JENSEN, H. L., 1942.—Nitrogen Fixation in Leguminous Plants. I. *PROC. LINN. SOC. N.S.W.*, 67: 98-108.

————, and BERRY, R. C., 1943.—Nitrogen Fixation in Leguminous Plants. III. Ibid., 68: 1-8.

————, 1943.—Nitrogen Fixation in Leguminous Plants. IV. Ibid., 68: 207-220.

————, 1944.—Nitrogen Fixation in Leguminous Plants. V. Ibid., 69: 229-237.

————, 1945.—Nitrogen Fixation in Leguminous Plants. VI. Ibid., 70: 203-210.

JONES, F. R., and TISDALE, W. B., 1921.—Effect of Soil Temperature upon the Development of Nodules on the Roots of Certain Legumes. *J. Agric. Res.*, 22 : 17-32.

LEWIS, A. H., 1943.—The Teart Pastures of Somerset. III. *J. Agric. Sci.*, 33 : 58-63.

OERTEL, A. C., PRESCOTT, J. A., and STEPHENS, C. G., 1946.—The Influence of Soil Reaction on the Availability of Molybdenum to Subterranean Clover. *Aust. J. Sci.*, 9 : 27-28.

OLSEN, C., 1925.—Studies on the Growth of Some Danish Agricultural Plants in Soils with Different Concentration of Hydrogen Ions. *C.R. Trav. Lab. Carlsberg*, 16 (2) : 1-22.

PIPER, C. S., 1942.—Soil and Plant Analysis. (Adelaide.)

RICHARDSON, H. L., 1938.—The Nitrogen Cycle in Grassland Soils (etc.). *J. Agric. Sci.*, 28 : 73-121.

SNIESZKO, S., 1928.—L'influence exercée par la concentration des ions d'hydrogène du milieu nutritif (etc.). *Bul. Int. Acad. Polon. Sci., Cl. Sci. Math. Nat.*, B, Année 1928 : 55-74.

STEPHENS, C. G., and OERTEL, A. C., 1943.—Response of Plants to Molybdenum in Pot Experiments on the Cressey Shaley Clay-loam. *J. Counc. Sci. Industr. Res.* (Melbourne), 16 : 69-74.

THORNTON, H. G., and NICOL, H., 1936.—Reduction of Nodule Numbers and Growth, Produced by the Addition of Sodium Nitrate to Lucerne in Sand Culture. *J. Agric. Sci.*, 26 : 173-188.

VIRTANEN, A. I., 1928.—Ueber die Einwirkung der Bodenazidität auf das Wachstum und die Zusammensetzung der Leguminosepflanzen. *Biochem. Z.*, 193 : 300-312.

————, 1938.—Cattle Fodder and Human Nutrition. (Cambridge.)

WHITING, A. L., 1915.—A Biochemical Study of Nitrogen in Certain Legumes. *Ill. Agric. Exp. Stat. Bull.* No. 179 : 471-542.

WILSON, J. K., 1926.—Legume Bacteria Population of the Soil. *J. Amer. Soc. Agron.*, 18 : 911-919.

————, 1931.—Relative Numbers of Two Species of *Rhizobium* in Soils. *J. Agric. Res.*, 43 : 261-265.

WILSON, P. W., and Umbreit, W. W., 1937.—Fixation and Transfer of Nitrogen in the Soybeans. *Cent. Bakt.*, II, 96 : 403-411.

————, 1940.—The Biochemistry of Symbiotic Nitrogen Fixation. (Madison, Wis.)

————, and BURRIS, R. H., 1947.—The Mechanism of Biological Nitrogen Fixation. *Bact. Rev.*, 11 : 41-73.

WOZAK, H., 1929.—Stickstoffgehalt und Stickstoffverteilung in einigen Leguminosen (etc.). *Fortschr. Landw.*, 4 : 485-488.

ON AUSTRALIAN COLEOPTERA. PART I.

By J. W. T. ARMSTRONG.

(One Text-figure.)

[Read 24th September, 1947.]

INTRODUCTION.

This paper contains the results of an attempted study of the Australian species of the families Lagriidae and Pedilidae, which could not be completed owing to the reluctance or inability of several museums to send material on loan under wartime conditions. In the case of the genus *Ictystygna*, it would be necessary to examine the types, nearly all of which are not in Australia, to reach any finality. It was therefore necessary to return the C.S.I.R. collection, which contained the bulk of the material available to me, to Canberra, and postpone a complete revision of these families. The Ictistygninae of the Lagriidae greatly resemble the Pedilidae, but may be recognized by the closed fore coxal cavities. My thanks are due, amongst others, to Mr. K. C. McKeown and the entomologists of the C.S.I.R.

The second section consists of notes and observations on species belonging to various other families.

SECTION 1.

Family LAGRIIDAE.

Borchmann dealt with the classification of this family very fully on a world basis in 1936 (*Genera Insectorum*). For the benefit of Australian students, the five genera represented in this country may be readily distinguished as follows:

Key to Australian Genera.

1. Elytra wide, expanding considerably to about apical third; body obese. (Elytra confusedly and in some species rugosely punctate.) 2
   Elytra much narrower, but little, or not at all, expanded behind the shoulders; body normal or narrow 3
2. ♂ with antennae not at all serrate .... *Lagria* F.
   ♂ with 9th and 10th antennal joints conspicuously and sharply serrate .. *Ecnolagria* Borchm.
3. Elytra striate punctate; form Cistelid-like .... *Synatractus* Macl.
   Elytra confusedly punctate; form Pedilid-like 4
4. Prothorax distinctly longer than broad .... *Egestriomima* Champ.
   Prothorax not longer than broad. (Tibiae, especially the middle pair, denticulate or setulose externally.) .... *Ictistygna* Pasc.

Genus ECNOLAGRIA Borchmann.

Arch. f. Naturg., 81A (2), 1915, 49 and 139.

The following key, based on that given by Borchmann (*Gen. Ins.*, Fasc. 204, 1936, p. 141), should be of use to Australian coleopterists:

Key to the Australian species of Ecnolagria.

1. Posterior tibiae of ♂ without sexual characters, i.e., without one or more teeth on the inner margin 2
   Posterior tibiae of ♂ with one or more teeth on the inner margin 3
2. Colour dark; elytra metallic green or violet, very rugose. (Hab. W.A.) ....
   .... *aeneoviolacea* Champ.
   Colour much lighter; elytra reddish, much more finely punctate, each with two weak ribs
   .... *affinis* Bois.

3. Posterior tibiae of ♂ armed with a pronounced medial tooth on the inner margin 4
Posterior tibiae of ♂ armed with a row of teeth on the inner margin. (Colour much as in
grandis.) 5
4. Upper surface predominantly or entirely stramineous or light reddish-brown; basal
abdominal segment of ♂ acutely carinate .... grandis Gyll. (= rufescens Bois.)
Head and pronotum blue-black, scutellum yellowish, anterior third of elytra blue followed
by a gold band then the remainder purple; posterior femora of ♂ strongly thickened
and widely excavated beneath; posterior tibiae of ♂ also excavated for first third,
second third, flat and triangularly widened and with a fairly long pointed tooth
.... aurofasciata Borchm.
5. Posterior tibiae of ♂ coarsely toothed; first segment of abdomen carinate, second last with
a tubercle on hind margin .... serripes Borchm.
Posterior tibiae of ♂ very finely toothed; first segment of abdomen not carinate ....
.... tomentosa F. (= pulchrivaria Lea)

Genus EGESTRIOMIMA Champion.

Trans. Ent. Soc. Lond., 1916, Pt. 2, 183.

To date this genus has been represented by only two species, *E. albiliniata* Cart., originally described as an *Egestria* (PROC. LINN. SOC. N.S.W., 1905, p. 189), and *E. fulvipennis* Champ., described at the same time as the genus. Both these species are before me. Two more are now described. *Selenopalpus fuscus* Macl., discussed below, also very probably belongs to this genus.

The four species may be tabulated thus:

1. Clothing black or piceus patterned with ashy-white .... albiliniata Cart.
Clothing not thus 2
2. Form broader, especially the head; cuticle of elytra wholly black .... carteri, n. sp.
Form narrower; cuticle of elytra wholly or mainly testaceous 3
3. Legs and abdomen black; anterior medial depression of head stronger .. fulvipennis Champ.
Legs and abdomen castaneous; anterior medial depression of head not so strong ....
.... castaneiventris, n. sp.

EGESTRIOMIMA CARTERI, n. sp.

Elongate, nitid, black, antennae, anterior tibiae and tarsi, and palpi obscurely testaceous, dorsal surface thickly clothed with stramineous depressed pubescence, patterned on each elytron with an oblique cinerescent vitta commencing at the shoulders and fading out medially just before the apex, suture also narrowly cinerescent, the whole intermixed with long semi-erect dark hairs, clothing of ventral surface cinerescent.

Head slightly longer than greatest width at eyes, basal angles rounded, sides expanding a little to eyes, medially broadly flattened, somewhat depressed in front of eyes, with variable and fairly close punctures. Antennae slender, segments gradually decreasing in length after second. Pronotum as wide as head behind eyes, a little longer than wide, subcylindrical, sides medially constricted, finely punctate, narrowly and definitely caniculate on disc. Elytra not quite twice as long as prothorax, twice as long as wide, expanding slightly for two-thirds of length, apices evenly rounded, coarsely but not very closely punctate.

Size: 8 mm. × 2·5 mm.

Hab.—N.S.W., Telegraph Point (H. J. Carter and J. Armstrong), Hastings R. (H. J. Davidson).

Type from Telegraph Pt. in Carter Coll., C.S.I.R.; paratypes in those of H. J. Davidson and the author.

The key given above should suffice to differentiate this species from the others of the genus. Of the four specimens before me, three from Telegraph Pt. on the North Coast are identical, but that from Hastings R. has all its legs fusco-testaceous. They all appear to be females.

EGESTRIOMIMA CASTANEIVENTRIS, n. sp.

Elongate, nitid, mainly castaneous, head excluding mandibles, palpi, antennae and penultimate tarsal joint black, thorax and underside with a varying amount of black, elytra testaceous but infuscate at suture on basal half of type specimen, dorsal surface thickly clothed with depressed stramineous pubescence interspersed with longer semi-erect darker hairs, clothing of underside pallid.

Head half again as long as width at eyes and almost parallel behind them, broadly flattened and somewhat depressed in front of eyes, rather closely punctate, punctures variable in size. Antennae slender, segments gradually decreasing in length after the second. Prothorax as wide as head across eyes, half as long again as wide, subcylindrical, sides medially constricted, finely punctate, obscurely caniculate on disc. Elytra not quite twice as wide as prothorax, two and a half times as long as wide, sides parallel for two-thirds length, apices evenly rounded, coarsely but not very closely punctate. Fifth ventral segment of ♂ deeply excavate down middle and deeply emarginate at apex.

Size: 10·5 mm. × 2·5 mm.

Hab.—N.S.W., Ropes Cr., Nov., 1939 (H. J. Carter), Rivertree (E. Sutton), French's Forest (H. Davidson).

Holotype from Ropes Cr. in Carter Coll., C.S.I.R., allotype and paratype in the author's coll., paratype in H. Davidson's coll.

There are four specimens before me. As stated above, the amount of black on the body varies, but is mostly concentrated on the disc of the prothorax and on the metasternum. The species is very close to *E. fulvipennis* Champ. and was so identified by H. J. Carter, but in addition to colour differences, the prothorax is less constricted at middle and the head less flattened. I have specimens of Champion's species from the Bogan and Peel Rivers, N.S.W.

Family LAGRIIDAE (Species wrongly included in Oedemeridae).

Two species described by Macleay (*Trans. Ent. Soc. N.S.W.*, 1866, II: 311–2) as belonging to the genus *Selenopalpus* of the Oedemeridae do not belong to that family but are almost certainly Lagriids. Unfortunately both types are unique. I believe *S. mastersi* to be close to, if not identical with, *Ictistygna fasciata* Champ. McKeown writes that it fits Champion's description very well and could quite easily be the same species. *S. fuscus* is almost certainly an *Egestriomima*, but, having not seen the type since studying the genus, I am unable to place it in the key given above. Specimens of the other species of *Egestriomima* were submitted, for comparison, to McKeown, who writes that none of them are close enough in his opinion. It is hoped to clear this matter up later.

Family PEDILIDAE.

Key to Australian Genera.

1. Upper surface tuberculate, eyes very prominent. (Neck not at all visible from above.)
   .... *Anaplopus* Blackb.
   Not as above 2

2. Neck very narrow; maxillary palpi serrate. (Last 3 joints of antennae longer and wider than those preceding.) .... *Macratria* Newm.
   Neck comparatively wide; maxillary palpi not serrate 3

3. Terminal joint of maxillary palpi securiform. (Upper surface very coarsely punctate; terminal joint of ♂ antennae elongate.) .... *Diacalla* Pasc.
   Terminal joint of maxillary palpi cultriform. (Upper surface more finely punctate; terminal joint of ♂ antennae elongate, except in *E. suturalis* Pasc.) .... *Egestria* Pasc.
   Terminal joint of maxillary palpi oblong, subtriangular. (Terminal joint of ♂ antennae ovate.) .... *Egestrina* Champ.
   Terminal joint of maxillary palpi ovate. (♂ with post tibiae prominently armed on inner margins.) .... *Macratriamima* Champ.

Genus EGESTRIA Pascoe.

Champion (*Trans. Ent. Soc. Lond.*, 1916, 194–5) only recognized two species, *E. suturalis* Pasc. and *E. taeniata* Pasc., of this genus, placing *E. griseolineata* Fair. and *E. pallitibra* Fair. as synonyms of the latter. In case of *griseolineata* I believe he was mistaken.

Four species are represented in the material before me, including one, of which I have taken numerous specimens in the Bogan R. district of N.S.W., that agrees very well with Fairmair's brief description of *E. griseoliniata*. It differs from *E. taeniata*

---

* Unknown to me in nature but must be very close to *Egestria*.

Pasc. *inter alia*, in having noticeably stouter antennae and tarsi, the former noticeably serrate in the ♂. It is not so dark, less shining and more heavily clothed. A long series of *E. taeniata* from the same locality, agrees with Pascoe's description in the case of the female while the male is evidently the insect on which Fairmair's description of *E. pallitibra* was based. They have some noticeable long black hairs at the basal angles of the head. The fourth species appears to be new and is described hereunder.

The four species may be tabulated thus:

1. Apical joint of antennae not elongate in either sex; elytra with white pubescence densest at suture .... *suturalis* Pasc.
   Apical joint of antennae at least as long as the two preceding; pale pubescence forming a more or less distinct vitta on each elytron 2
2. Antennae and tarsi stouter, the former serrate in ♂; elytral markings well defined ......
   .... *griscoliniata* Fairm.
   Antennae and tarsi slender, the former filiform in both sexes; elytral markings not so definite 3
3. Apical joint of antennae as long as three preceding in ♂ and as two preceding in ♀ ....
   .... *taeniata* Pasc.
   Apical joint of antennae longer than the six preceding in ♂ and as long as the five preceding in ♀ .... *antennalis*, n. sp.

EGESTRIA ANTENNALIS, n. sp.

♂. Elongate, black, elytra and second, third and fourth abdominal sternites ferrugino-testaceous, tibiae, tarsi and joints 3 to 10 of antennae ferrugineous; clothed with pale semi-erect pubescence, becoming testaceous on head and sides and apex of elytra, each elytron with a wide oblique vitta from shoulder to suture just in front of apex (as in *E. taeniata*) of griseus more depressed pubescence.

Head transverse, moderately and confluently punctate. Pronotum elongate, expanded a little before middle, not quite as wide as head, finely and closely punctate with a medial line traceable from base to neck. Scutellum densely pubescent. Elytra wider than prothorax, twice as wide as base thereof, shoulders rounded, sides thence gradually narrowing towards apex, this evenly rounded, not so closely nor so finely punctate as pronotum. Antennae, joint 2 shorter than 1, 3 and 4 almost twice as long as 2, 5 to 10 becoming progressively shorter, 11 subcylindrical, slightly bent at middle, and longer than preceding six together.

Size: 9 mm. × 2·25 mm.

♀. Darker. Elytra fuscopiceous, sides parallel. Abdominal sternites dark. Antennae with terminal joint thinner from middle to apex and as long as preceding five together.

Size: 11 mm. × 3 mm.

Hab.—South Queensland, Milmerran (J. Macqueen).

Holotype and allotype in the Australian Museum, paratype in the C.S.I.R. Coll.

Three specimens, including the sexes, taken during December, 1926, represent a species that is very similar to *E. taeniata* but is at once distinguished from that species by the longer terminal joint of the antennae in both sexes. The antennae are not quite so slender; its form is rather more robust and the punctures of the pronotum are finer and closer. As mentioned previously, the ♂ of Pascoe's species has black hairs on the head.

MACROTRIOMIMA LONGIGERA Champ.

Trans. Ent. Soc. Lond., 1916, 167.

Five specimens, two from N.S.W. and three from Western Australia, cannot be sufficiently differentiated from the description of this species to be regarded as distinct, though the posterior tibiae are less strongly curved than in Champion's figure. The colour of the legs is variable, being red in two New South Wales and one Western Australian specimen and darker, almost black, in the other two Western Australian specimens with the exception of the anterior tibiae. The clothing is stramineous on the New South Wales specimens and griseus on those from Western Australia. The species was described from New Guinea.

MACRATRIA DAVIDSONAE, n. sp. Text-fig. 1.

Elongate, uniformly castaneous, nitid, rather sparsely clothed with depressed golden pubescence, becoming thicker at the tibiae and tarsi, and with occasional longer, fine, erect setae.

Head slightly longer than wide with two shallow depressions between base of eyes connecting with a short sulcus at base, finely and closely punctate; eyes large. Antennae long, about half length of insect, slender, joints 9 to 11 thicker cylindrical, 9 and 10 each as long as 6 and 8 combined, 11 not quite as long as 9 and 10 combined. Prothorax very long, three-fifths as wide as long, not quite as wide as head, widening to just
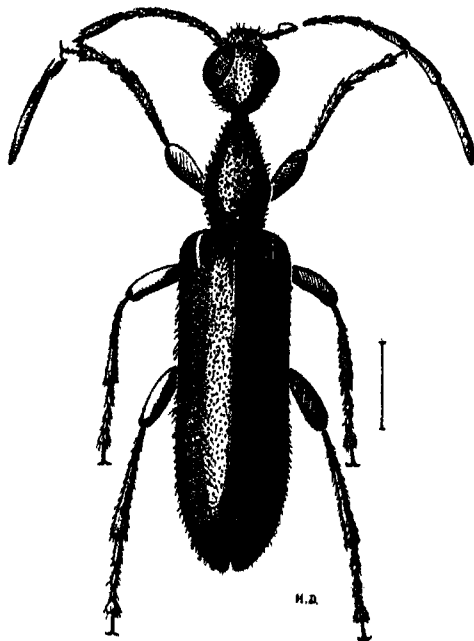
Text-fig. 1.—*Macratria davidsonae*, n. sp.

before middle then narrowing uniformly to apex, disc subconvex, fairly closely and finely punctate. Elytra three times as long as wide, slightly over half as wide again as prothorax, almost parallel sided, very slightly narrowed hindwards, suture raised after basal fourth, a small elongate basal depression inside each shoulder, closely and finely punctate, punctures becoming still finer towards apex and are not at all linear in disposition (they are closer than indicated in the figure). First joint of anterior tarsi enlarged, about as wide as the tibia and as long as the two following joints combined, densely pubescent beneath.

Size: 9 mm. × 2 mm.

Hab.—N.S.W., Acacia Plateau (Davidson).

Type unique in the author's coll.

This very large species, of which there is a single example before me, does not come near any Australian species known to me or of which I have seen the description. It is to be noted that I have not seen the descriptions of Pic's two Australian species *M. bangaasi* and *M. pallidiceps*, which are not available in this country. Champion (*Trans. Ent. Soc. Lond.*, 1916, 201) mentions the enlarged basal joint of the anterior tarsi as a character to be found in certain tropical American forms. I have to thank my friend H. J. Davidson for permission to describe this insect and also for the accompanying figure. It is named after Mrs. Davidson, whose ability as a collector led to its capture.

SECTION 2.

Some miscellaneous notes on species of various families.

Family CUPIDAE.

OMMA MASTERSI Macl.

Trans. Ent. Soc. N.S.W., II, 1866, 169.

A fine example of this species, taken on the bank of the Bogan River between Nyngan and Dandaloo, N.S.W., indicates that, though rare in collections (the only other specimen known to me, is the type from Gayndah, Q.), the species is widespread. The black and white scales are so arranged as to give a striking resemblance to the female of one of the commoner species of Mutillid wasps.

Family COLYDIIDAE.

NEOTRICHUS ACANTHACOLLIS C. and Z.

PROC. LINN. SOC. N.S.W., lxii, 1937, 195, Pl. ix, fig. 15.

A series of specimens of this beetle was taken by me, at the end of December, 1945, on a species of *Loranthus* (mistletoe) growing on "stringy-bark" (*Eucalyptus* sp.) at Inverell, N.S.W. The beetles were confined to the mistletoe, occurring on a number of different plants, so may breed in the dead twigs. Mr. McKeown, of the Australian Museum, kindly compared specimens with the unique type which is abraded. Fresh specimens are clothed with broad, short, depressed scales, interspersed with groups of darker, erect, stout, blunt hairs, the latter disposed principally along the pronotal prominences, in tufts on the elytra and as a tuft over each eye, with a lighter coloured row in the vicinity of the clypeal suture. The flat scales are cinerescent fulvous and brown, and form a complicated pattern, but are almost entirely fulvous on the sides of the prothorax.

Family BOSTRYCHIDAE.

XYLABOSCA LEAI Lesne.

Ann. Soc. Ent. Fr., 1900, 570.

Lea (PROC. LINN. SOC. N.S.W., xxxvi, 1911, 474) places this species as a synonym of *X. bispinosa* Macl. without giving any reason. I have seen several specimens, including one identified by Lea himself, that are quite evidently distinct from *X. bispinosa* by reason of the fringe of long hairs on the head and the front of the pronotum being distinctly concave when viewed from above. There is a specimen in the Tasmanian Museum that appears to be the ♂ of this species. It has the above-mentioned characters in addition to which the elytra are shorter and the apical declivity more abruptly flattened than in *X. bispinosa.* The two apical spines are longer and more slender and for the first half of their length they are almost parallel, then rapidly diverge so as finally to be almost at right angles.

XYLABOSCA HIRTICOLLIS Blackb.

Trans. Roy. Soc. S.A., 1897, 92.

This species, described from Western Australia, extends to New South Wales. An example was recently taken by me on the Bogan River above Nyngan.

Family BYRRHIDAE.

BYRRHINUS PUBIVENTRIS Lea.

Rec. S. Aust. Mus., 1920, i, 277.

Seven specimens, evidently part of the original series taken by Helms on the Upper Ord River, N.W. Australia, submitted to me for identification by Mr. Scott of the Western Australian Department of Agriculture, have the upper surface pubescent except where it is obviously abraded. Two specimens are almost completely clothed. When he described the upper surface as glabrous, Lea was deceived by the uniform abrasion of the three specimens in the type series.

x

Family HISTERIDAE (Species wrongly included in Corylophidae).

Acritus sternalis Lea = *Ittrion prosternalis* Deane, n. syn.

Examination of a series of *Ittrion prosternalis* Deane (including a cotype), which was referred by its author to the Corylophidae, has convinced me that the insect belongs to the Histeridae. It was described and figured (PROC. LINN. SOC. N.S.W., 1932, 334) from material collected by myself. A comparison with the description of *Acritus sternalis* Lea (*Trans. Ent. Soc. Lond.*, 1925, 262) leaves little doubt that it is synonymous with that species. In Deane's figure the tarsi appear to be four-segmented, but this is the case only with the hind pair. Under the microscope, using a fairly high power, the 10th and 11th antennal joints can be perceived in the compact club.

Family BUPRESTIDAE.

NEOBUPRESTIS TRISULCATA Cart.

PROC. LINN. SOC. N.S.W., lvii, 1932, 102.

My collection contains a pair of this species, taken within a mile of the type locality. The description was based on a single ♀ which was stated to be glabrous. In fresh examples this is not so, as the pronotal sulci have the punctures filled with a white meal, which is also present on the head and in spots on the elytra placed in a basal, medial, and sub-apical zone and as a double post-medial spot on either side of the suture.

The ♂ is similar to the ♀ except that the legs are much stouter, especially the medial pair, in which the tibia is thickened to approximately the same size as the femur. It is much smaller.

Size: 11·5 × 4 mm.

Allotype ♂ in the author's collection.

HYPOCISSEIS ORNATA Cart.

PROC. LINN. SOC. N.S.W., xlviii, 1923, 175.

In December, 1945, about 20 specimens of this species were taken by me on a species of *Loranthus* (mistletoe) growing on "stringy-bark" (*Eucalyptus* sp.) near Inverell, N.S.W. A pair were also taken some years ago from another species of *Loranthus* on the Bogan River, N.S.W.

CASTLARINA BOGANIA Cart.

PROC. LINN. SOC. N.S.W., lv, 1930, 534.

Since this species was described, a number of specimens have been taken every year, during November, on the flowers of *Myoporum platycarpum*; only very rarely on other flowers out at the same time. My thanks are due to Mr. R. H. Anderson, of the Botanic Gardens, Sydney, for the botanical name.

THE INFLUENCE OF MOLYBDENUM, CALCIUM AND AGAR ON NITROGEN FIXATION BY *AZOTOBACTER INDICUM*.

By H. L. Jensen, formerly Macleay Bacteriologist to the Society.*
(*From the Department of Bacteriology, University of Sydney.*)

(Plate xxiii; two Text-figures.)

[Read 26th November, 1947.]

Introduction.

Azotobacter indicum Starkey and De (1939) was isolated from rice soils in India and was found to grow and fix nitrogen over a range of reaction from pH about 3 to about 9 (Starkey, 1939). It thus forms a remarkable contrast to other species of *Azotobacter* in which nitrogen fixation ceases at pH 6 and less (e.g., Burk *et al.*, 1934). It is not known whether *Az. indicum* also occupies a special position with regard to molybdenum (or vanadium), which is essential or at least stimulating for nitrogen fixation by other *Azotobacter* species (e.g., Horner *et al.*, 1942), and calcium, which appears to be a generally essential element (Krzemieniewska, 1910; Burk and Lineweaver, 1931; Horner and Burk, 1934; Burk and Burris, 1941). Some experiments in this direction have been made with a strain of *Az. indicum* kindly supplied to me by Dr. R. L. Starkey, New Jersey Agricultural Experiment Station, New Brunswick, N.J., U.S.A.

Methods.

The basal medium had the following composition, unless otherwise stated: carbon compound (mostly sucrose), 20·0 gm.; K_2HPO_4, 0·25 gm.; KH_2PO_4, 0·25 gm.; $MgSO_4$, 0·2 gm.; NaCl, 0·2 gm.; $FeSO_4$, 0·02 gm.; distilled water, 1,000 ml. Calcium, usually as chloride, and molybdenum, as sodium molybdate, were added in varying concentration. The salts were of ordinary analytical purity. Duplicate, or sometimes triplicate, cultures were grown in 25 ml. medium in 250-c.c. Erlenmeyer flasks or round flasks of Pyrex glass; the former gave more rapid growth, probably owing to the larger surface area of the liquid (cf. Wilson and Burris, 1947), but upon the whole the growth in favourable media was very vigorous and accompanied by abundant mucus formation, which after a few weeks gave the cultures the appearance of a flour-paste. Incubation took place at 30–32°C., in some cases 35–36°C.; the temperature seemed to make little difference within these limits. Nitrogen was determined by the Kjeldahl method, with selenium as a catalyst and n/28 sulphuric acid and sodium hydroxide for the titration. The whole culture was analysed, except in a few instances, when an aliquot was taken for glucose determination by the method of Lane and Eynon. The nitrogen content of cultures analysed immediately after inoculation was subtracted from that of the incubated cultures to give the net gain of nitrogen, which in the subsequent tables is always expressed as mgm. per 25 ml. medium. Control cultures of *Pseudomonas pyocyanea, Rhizobium meliloti* and *Aspergillus niger*, incubated together with the cultures of *Azotobacter*, showed after two to four weeks mere traces of growth and no significant gains of nitrogen (less than 0·1 mgm.); assimilation of combined nitrogen from the incubator-atmosphere may thus be practically disregarded. The inoculum of *Az. indicum* consisted of a drop of cell suspension from young agar slope cultures, or of liquid cultures in Mo- or Ca-free solution when these elements were to be tested.

* State Laboratory of Plant Culture (Department of Bacteriology), Lyngby, Denmark.

EXPERIMENTAL RESULTS.

Preliminary Tests. Very little nitrogen (0·1 to 0·7 mgm. per flask in 14 or 15 days) was fixed in glucose or sucrose medium to which no molybdenum was added. The fixation rose to 4·0–6·5 mgm. in medium with 5 parts per million of sodium molybdate, but the same quantity of vanadium sulphate or ammonium vanadate had no effect. Nitrogen fixation was equally strong in the presence and absence of 0·025% calcium chloride; 0·2% potassium oxalate had no inhibitory effect on *Az. indicum,* although it completely suppressed nitrogen fixation by *Az. chroococcum.* In subsequent experiments, where molybdenum was not the factor tested, 5 p.p.m. sodium molybdate (= 2·4 p.p.m. Mo) was added; calcium was only added where actually stated.

Various organic growth factors, such as pure biotin, potato extract, lucerne-root extract and soil extract, did not significantly increase nitrogen fixation, but 0·1% agar had a conspicuous effect on the fixation, which in ten days amounted to 9·5–10·0 mgm. in medium with agar, against 1·5–2·3 mgm. in control medium (cf. Rippel, 1936).

Qualitative tests with various sources of carbon (organic acids as sodium salts) showed no growth, or trace only, with butyl alcohol, butyric acid, valeric acid, citric acid, xylose, maltose, lactose, and starch. Scant growth was produced with ethyl alcohol, acetic acid, and lactic acid, but fair to good growth with glycerol, mannitol, sorbitol, succinic acid, malic acid, arabinose, glucose, levulose, galactose, sucrose, raffinose, and inulin.

Experiments with Molybdenum. The source of carbon in these tests was commercial sucrose (ordinary white table sugar), which previous experiments with *Az. chroococcum* had shown to be very poor in available molybdenum and/or vanadium, and which was further purified by filtration through animal charcoal (cf. Horner *et al.*, 1942). In the first experiment a strongly nitrogen-fixing strain of *Az. chroococcum* was grown in medium with 0·1% calcium carbonate for comparison with *Az. indicum.*

The figures in Table 1 show that both species fix only a very small, and *Az. indicum* hardly a significant, amount of nitrogen in the molybdenum-free medium. The stimulating effect of molybednum on *Az. indicum* begins at a concentration of 0·1 to 1·0γ per litre, and increases with some irregularity up to 1 mgm. per litre. Vanadium is entirely without effect. It is further noteworthy that the omission of calcium carbonate from the medium causes almost complete cessation of the nitrogen fixation by *Az. chroococcum*, while *Az. indicum* grows well in the calcium-free medium with sufficient molybdenum concentration. Its growth, however, is much slower than that of *Az. chroococcum.*

Higher concentrations of molybdenum, and another form of vanadium, were tested in a second experiment, recorded in Table 2. The gains of nitrogen are somewhat higher and more consistent than in Table 1, and the optimum seems to be reached at a molybdenum concentration of 0·1 p.p.m. Vanadium is ineffective also as sulphate. These results show clearly that the nitrogen-fixing enzyme system of *Az. indicum* resembles that of other *Azotobacter* species in so far as molybdenum is stimulatory and apparently essential for its activity, but it differs by not responding to vanadium; in this respect *Az. indicum* resembles several strains of nitrogen-fixing clostridia (Jensen and Spencer, 1947).

Experiments with Calcium. Media with pure sucrose (Gurr, "Bacteriological") and glucose (Mallinckrodt) were first tested, with increasing doses of calcium chloride. An attempt was made to purify the sucrose medium further by the procedure of Waring and Werkman (1942): repeated addition of 8-hydroxyquinoline and extraction with chloroform at pH 10. (According to Prodinger (1940), calcium is completely precipitated by 8-hydroxyquinoline at pH 9·2 and above.) This, however, proved unsuccessful; less than 0·1 mgm. Ca was extracted from a solution of 20 gm. commercial sucrose which by direct analysis was found to contain approximately 0·5 mgm. Ca.

As shown in Table 3, vigorous growth and nitrogen fixation took place, but calcium has no stimulating effect; neither is there any sign of inhibition by calcium carbonate

TABLE 1.

Effect of Molybdenum on Nitrogen Fixation by Azotobacter indicum and Azotobacter chroococcum.

Az. indicum.		Az. chroococcum.	
Medium.	Gain of N, mgm. per Culture.	Medium (+0·1% CaCO₃).	Gain of N, mgm. per Culture.
Control (−Mo)	0·09–0·11	Control (−Mo)	0·19–0·23
0·0001 p.p.m. Mo	0·20–0·20		
0·001 ,, ,.	0·38–0·59	0·001 p.p.m. Mo	0·34–0·44
0·002 ,, ,,	0·73–0·75		
0·005 ,, ,,	0·83–1·04		
0·01 ,, ,,	1·56–2·32		
0·05 ,, ,,	1·74–2·42		
0·1 ,, ,,	1·35–1·53		
1·0 ,, ,,	2·25–3·93	1·0 p.p.m. Mo	7·81–8·03
0·2 ,, V	0·08–0·10	(1·0 ,, ,, −CaCO₃)	0·14–0·24
2·0 ,, ,,	0·07–0·11		

25 ml. sucrose medium in 250 c.c. round flasks. Initial N-content, 0·08 mgm. Incubation 18 days 35° C. (Az. chroococcum 8 days). Vanadium as NH₄VO₃.

TABLE 2.

Effect of Molybdenum on Nitrogen Fixation by Azotobacter indicum.

Medium.	Gain of N, mgm. per Culture.
Control (−Mo)	0·13–0·14
0·1 p.p.m. Mo	3·81–4·10
1·0 ,, ,,	3·65–4·28
5·0 ,, ,,	3·60–3·69
10·0 ,, ,,	4·14–4·48
1·0 ,, V (as VOSO₄)	0·16–0·19

25 ml. sucrose medium in 250 c.c. round flasks. Initial N-content, 0·07 mgm. Incubation 21 days 30–32° C.

in the glucose medium, as reported by Starkey (1939). It thus appears that calcium is neither essential nor stimulatory, or else the impurities of the medium must have been sufficient.

The calcium content of the sugars was determined by ashing 30 gm. sugar in a silica basin and taking up the minute residue in a small volume of hot dilute hydrochloric acid from which the calcium was precipitated with ammonium oxalate at pH 5. The precipitate was collected and washed by centrifugation, and calcium was determined by titration with n/20 potassium permanganate, using a microburette with 0·01 ml. divisions. The glucose and the sucrose were found to contain 0·20 and 0·23 mgm. Ca, respectively, in 30 gm. The sugars thus impart contents of 0·13 and 0·16 p.p.m. calcium to the medium when added in amounts of 20 gm. per litre. These quantities together with the possible impurities of the other constituents thus seem fully to cover the calcium requirements (if any) of Az. indicum.

A more purified medium was made up in the following way. Concentrated solutions (1/20 of the final volume) were prepared in two portions, the phosphate being kept separate from the rest of the constituents, sufficient potassium oxalate was added to give a final concentration of 0·1%, the solutions were left overnight, the slight precipitates were removed by centrifugation, and the medium was finally made up to

volume with triple-distilled water as used for blood transfusion. The phosphate was supplied as sodium salts in order to avoid ionic imbalance. Calcium was added as 0·1% calcium chloride, which suffices to precipitate the oxalate and leave a small surplus of calcium in the solution.

The results, which are given in Table 5, show good growth in the calcium-free medium and no beneficial effect of the calcium; in fact, one culture in glucose medium shows an inexplicable reduction in nitrogen fixation.

TABLE 3.

Nitrogen Fixation by Azotobacter indicum *in Medium with varying Calcium Content.*

Sucrose Medium.	Gain of N, mgm. per Culture.	Glucose Medium.	Gain of N, mgm. per Culture.
Control (–Ca)	3·39–3·42	Control (–Ca)	6·51–7·09
20 p.p.m. Ca	2·46–2·78	10 p.p.m. Ca	5·63–6·11
100 ,, ,,	3·51–4·15	100 ,, ,,	6·01–6·29
250 , ,,	3·88–3·93	250 ,, ,,	5·27–5·76
500 ,, ,,	2·55–2·85	250 ,, ,, (as CaCO₃)	6·82–lost

Sucrose medium: 25 ml. in 250 c.c. round flasks. Initial N-content, 0·06 mgm. Incubation 20 d. 30–32° C. Glucose-medium: 25 ml. in 250 c.c. Erlenmeyer flasks. Initial N-content, 0·06 mgm. Incubation 19 d. 30–32° C.

TABLE 4.

Nitrogen Fixation by Azotobacter indicum *in Oxalate-purified Medium.*

	Glucose Medium.		Sucrose Medium.	
	Control (–Ca).	+0·1% CaCl₂.	Control (–Ca).	+0·1% CaCl₂.
Gain of N, mgm. per culture—				
a ..	7·70	7·72	9·22	8·52
b ..	7·88	(3·92)	9·47	7·33
c ..	7·29	7·49	9·60	9·46
Mean ..	7·6	6·4 (7·6)	9·4	8·6

25 ml. medium in 250 c.c. Erlenmeyer flasks. Initial N-content, 0·07 mgm. (glucose), 0·10 mgm. (sucrose). Incubation 18 days. 30° C.

To eliminate the possible effect of the small amount of calcium remaining in solution as oxalate, an experiment was performed in medium made up with triple-distilled water and extra pure glycerol, distilled *in vacuo* from A.R. grade glycerol, which could be regarded as practically free from calcium. Since glycerol is only a moderately good source of carbon, 3% was given instead of the customary 2%, and the cultures were incubated for four weeks. The results in Table 5 show vigorous nitrogen fixation in the calcium-free medium and, except for a remarkably high gain in one of the cultures with 100 p.p.m. Ca, no stimulating effect of calcium chloride. Calcium carbonate, at least in the higher dose, shows in this case a definite inhibitory effect.

A final experiment was designed to provide for the possibility of small amounts of calcium coming into solution from the Pyrex glass, which was stated by the manufacturers to contain only 0·4% CaO. The cultures were grown in silica evaporation dishes of 9 cm. diameter, covered with Petri dish lids. The medium contained 2% vacuum-distilled glycerol; one portion had the customary composition and was given

two concentrations of calcium chloride; another portion was made up with sodium phosphate and potassium oxalate as above (no visible precipitate appeared). The result of this test is seen in Table 6. The growth in the oxalate-treated medium was slow and irregular, but good in the plain medium, and in both cases the addition of calcium shows no effect.

It seems justified to conclude that calcium is neither essential nor stimulatory for nitrogen fixation by *Az. indicum*, or else quite infinitesimal amounts must be sufficient for maximum yield. In this respect as well as with regard to reaction *Az. indicum* thus differs strikingly from *Az. chroococcum*, which for optimum nitrogen fixation requires a supply of 0·3–0·4 mgm. calcium per gm. glucose (Krzemieniewska, 1910).

TABLE 5.
Nitrogen Fixation by Azotobacter indicum in Pure Glycerol Medium.

Medium.	Gain of N, mgm. per Culture.
Control (–Ca)	3·91–4·05
10 p.p.m. Ca as CaCl₂	3·77–3·85
100 ,, ,, ,, ,,	3·90–5·60
250 ,, ,, ,, ,,	3·38–3·70
160 ,, ,, ,, CaCO₃	2·87–3·03
500 ,, ,, ,, ,,	1·82–2·57

25 ml. 3% glycerol medium in 250 c.c. Erlenmeyer flasks. Initial N-content, 0·05 mgm. Incubation, 28 days 30–32° C.

TABLE 6.
Nitrogen Fixation by Azotobacter indicum in Glycerol Medium with and without Oxalate.

Medium.	Gain of N, mgm. per Culture.
Plain, –Ca	4·28–4·72
,, 10 p.p.m. Ca	4·22–4·37
,, 100 ,, ,,	2·82–4·10
Oxalate-purified, –Ca	1·23–2·04–2·59
,, ,, +0·1% CaCl₂	0·52–2·87–2·88

25 ml. glycerol medium in silica basins. Initial N-content, 0·08 mgm. Incubation, 21 d. 30–33° C.

Experiments with Agar. The effect of agar, observed in the preliminary tests, was studied in more detail in the customary medium with sucrose and 0·1% fibrous agar. Two other colloidal substances, soluble starch and pectin (commercial, from citrus fruits), were also tried, and a test with calcium carbonate was included. The results are seen in Table 7. Corrections were made for the small amounts of nitrogen present as impurities in starch (0·07%), agar (0·14%) and pectin (0·38%).

The accelerating effect of agar on the growth is very striking, especially after ten days. Starch has a similar but lesser effect, while pectin is inactive. Calcium carbonate seems to have no significant influence in this case.

Another experiment with starch (Table 8) confirms the small stimulating effect of starch in comparison with agar, and shows that the starch itself does not serve as material for nitrogen fixation.

The fact that *Az. indicum* is not stimulated by various organic substances, as observed in the preliminary tests, renders it unlikely that the effect of agar was due

TABLE 7.

Effect of Colloidal Substances and Calcium Carbonate on Nitrogen Fixation by Azotobacter indicum.

Medium.	Gain of N, mgm. per Culture, after		
	5 Days.	10 Days.	20 Days.
Control	0·61–0·62	2·08–2·29	4·82*–6·80
0·1% agar	1·18–1·74	7·23–8·08	10·56–10·81
0·2% starch		4·45–4·68	
0·5% pectin		2·04–2·07	
1·0% CaCO₃			5·71– 6·25

25 ml. sucrose medium in 250 c.c. Erlenmeyer flasks. Initial N-content of control medium, 0·05 mgm. Incubation at 30–32° C.

* Some ammonia was lost during the distillation.

TABLE 8.

Comparative Influence of Starch and Agar on Nitrogen Fixation by Azotobacter indicum.

Medium.	Gain of N, mgm. per Culture, after	
	8 Days.	18 Days.
Control	0·89–1·29	3·70–3·98
0·2% starch	0·90–1·08	4·24–5·30
0·4% „	1·19–1·23	4·91–5·09
0·1% agar	1·53–3·02	6·30–7·22
0·4% starch (–sucrose)		0·05–0·05

25 ml. sucrose medium in 250 c.c. round flasks. Initial N-content of control medium, 0·06 mgm. Incubation at 30–32° C.

to any growth compound or other organic impurity. However, an experiment was made with varying concentration of agar purified by maceration in water for five days at 30°C., extraction with dilute acetic acid, and washing with distilled water. The results in Table 9 show that the accelerating effect increases with the agar concentration, particularly from 0·1 to 0·2%. The purification has indeed lessened the effectiveness of the agar in comparison with the untreated material, but this may well be due to a notable loss of gel strength in the purified agar (cf. Rippel, 1936), and not necessarily to removal of impurities.

A final experiment was made in 2·5% glucose medium with 0·1% untreated agar; glucose consumption as well as nitrogen fixation was estimated. The bacterial substance was precipitated, together with the agar, by addition first of a 10% solution of aluminium chloride and then of sufficient normal sodium hydroxide to precipitate the aluminium as hydroxide, which carried down most of the slimy growth and the agar, where present. The precipitate was centrifuged down, the sediment was washed with distilled water, the centrifugate was made up to a definite volume, of which an aliquot was taken for glucose determination, and separate nitrogen determinations were made in the rest of the centrifugate and in the sediment. From 7 to 20% of the total nitrogen was found in the centrifugate, but this does not represent strictly extra-cellular nitrogen, since complete precipitation of the bacterial substance was difficult to obtain. Table 10 gives the results.

The economy of nitrogen fixation, 15 to 18 mgm. per gm. consumed sugar, is much the same as in other species of *Azotobacter*. The effect of the agar seems to

TABLE 9.

Influence of Varying Agar Concentration on Nitrogen Fixation by
Azotobacter indicum.

Medium.	Gain of N, mgm. per Culture.
Control (–agar)	3·33–3·34
0·05% agar, purified	4·84–5·14
0·1% ,, ,, ...	5·43–5·51
0·2 ,, ,, ...	7·95–8·18
0·4 ,, ,, ...	8·80–9·22
0·1% ,, untreated	8·30–8·32

25 ml. sucrose-medium in 250 c.c. Erlenmeyer flasks. Initial
N-content of control medium, 0·09 mgm. Incubation, 12 days 30–32° C.

TABLE 10.

Nitrogen Fixation and Glucose Consumption by Azotobacter indicum.

Medium	Control (–Agar).		+0·1% Agar.	
Incubation days	8	16	8	16
Gain of N, mgm. per culture—				
a	1·39	6·52	5·88	9·51
b	1·49	6·77	6·17	9·66
Consumption of glucose, mgm. per culture				
a	92	416	332	588
b	96	415	347	588
Mgm. N fixed per gm. glucose consumed				
a	15·1	15·8	17·7	16·2
b	15·5	16·3	17·8	16·4

25 ml. medium in 250 c.c. Erlenmeyer flasks. Initial N-content, 0·12 mgm. Incubation at 30–32° C.

consist in a simple growth acceleration, in agreement with the findings of Rippel (1936). The economy of fixation in the presence of agar is only slightly higher after eight days, and after sixteen days the difference has disappeared. It is noteworthy that in another case (Table 7) the economy appears even higher, reaching at least 21 mgm. nitrogen per gm. sucrose. The growth acceleration is probably, as in other species of *Azotobacter*, due to the physical effect of the agar, which supports growth near the surface of the medium and thus provides better access of oxygen and nitrogen than in the agar-free solution, where *Az. indicum* grows exclusively as a slimy bottom-deposit.

Growth with Combined Nitrogen. The growth rates in media with free and combined nitrogen were compared in order to see if the effect of molybdenum is a specific catalysis of the process of nitrogen fixation, as in other *Azotobacter* species.

Az. indicum was first grown in glucose medium with and without 5 p.p.m. sodium molybdate, with free nitrogen as well as with 400 p.p.m. nitrogen in the form of sodium nitrate and ammonium sulphate, this quantity corresponding approximately to the highest observed yield of fixed nitrogen. Duplicate cultures were grown in 15 ml. medium in 100-c.c. Erlenmeyer flasks and tested after 5, 10 and 14 days. The growth rate was estimated by turbidity measurements with a Hilger "Spekker" electrophotometer, and by determination of residual glucose.

The results are summarized in Text-figure 1. The growth with free nitrogen is notably stimulated by molybdenum, as in the previous experiments where nitrogen

was determined.   With nitrate the molybdenum appears to have, if anything, a
retarding effect, and with ammonium sulphate its effect is hardly significant; the very
poor growth in the last series was probably due to rapidly increasing acidity of the
medium: after 10 days the initial pH of 6·6–6·7 had fallen to 3·0–3·1, and this did not
change significantly after 14 days (pH 2·9–3·1).

Another experiment was performed in medium with combined nitrogen only, but
with two concentrations of molybdenum: 0·05 and 5·0 p.p.m. Mo. Calcium carbonate
(0·2%) was sterilized separately and added to the medium with ammonium sulphate
in order to prevent acidification, and was dissolved before the turbidity measurements
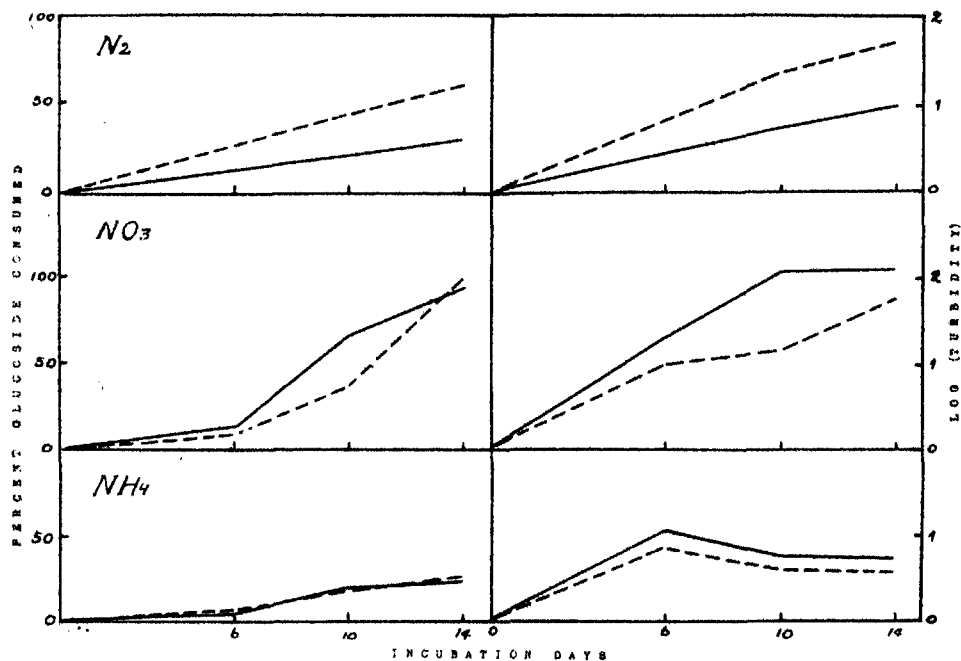
Fig. 1.—Influence of molybdenum on growth of *As. indicum* with free nitrogen, sodium
nitrate, and ammonium sulphate.   Left: sugar consumption.   Right: turbidity readings.
Continuous lines: –Mo; broken lines, 2·4 p.p.m. Mo.
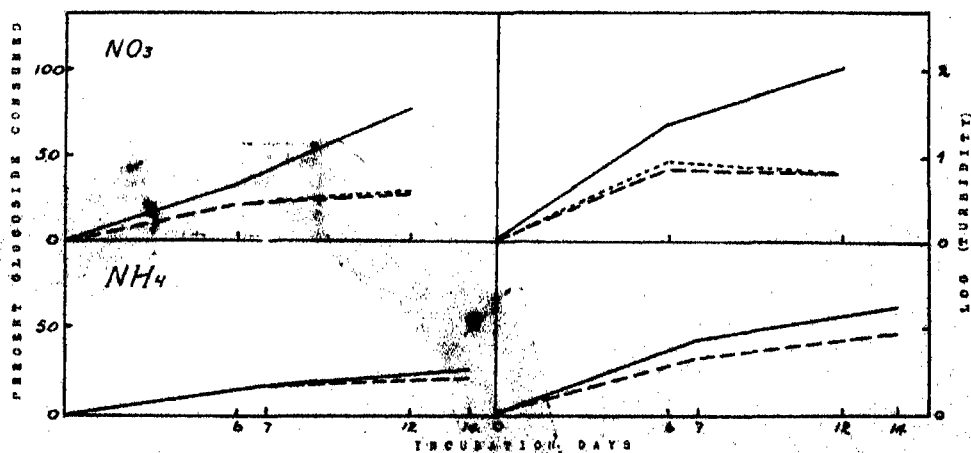
Fig. 2.—Influence of molybdenum on growth of *As. indicum* with sodium nitrate and
ammonium lactate.   Left: sugar consumption.   Right: turbidity readings.   Continuous lines:
–Mo; broken lines: 0·05 p.p.m. Mo; dotted lines: 5·0 p.p.m. Mo.

by addition of a small amount of hydrochloric acid. The inhibitory effect of molybdenum on growth with nitrate is in this case quite unmistakable, as shown in Text-figure 2. (It may here be mentioned that the sodium nitrate itself contained less than 0·1 p.p.m. Mo.) The growth with ammonium sulphate was extremely weak; the turbidity was barely visible, and only some 7 to 10% of the sugar was used up. No explanation for this remarkable inhibitory effect of the calcium carbonate can be offered. Another test was made, with nitrogen as ammonium lactate, and with 2·4 p.p.m. Mo, 20 ml. medium in 250-c.c. Erlenmeyer flasks, glucose and turbidity determinations after seven and fourteen days. The result is included in Text-figure 2, which shows that the moderately good growth with ammonium lactate is also somewhat retarded by molybdenum, although the effect on glucose consumption is not significant.

The ability of *Az. indicum* to utilize various forms of combined nitrogen was finally tested in molybdenum-free sucrose medium. Sodium nitrite, ammonium lactate, hydroxylamine (as hydrochloride), urea, glycine, alanine, asparagine, aspartic acid, glutamic acid and leucine were used in concentrations corresponding to 400 p.p.m. of nitrogen. The solutions of hydroxylamine-HCl, aspartic acid and glutamic acid were adjusted to original reaction (pH 6·6–6·7), and the solutions of hydroxylamine and urea were sterilized by Seitz-filtration instead of by autoclaving. Cultures with free nitrogen, in medium with and without 5 p.p.m. sodium molybdate, were included for comparison.

Table 11 gives the results, which show that aspartic acid is by far the best source of nitrogen, and the only one equal to elementary nitrogen (with molybdenum). Good growth is also produced with glutamic acid, leucine, and ammonium lactate, but asparagine is an inferior source of nitrogen, and urea gives little better growth than free nitrogen in the absence of molybdenum (cf. Starkey, 1939). The remaining four compounds are definitely inhibitory. This is hardly surprising in view of the relatively high concentration of reducing compounds like hydroxylamine and nitrite, but it is ⟍

TABLE 11.
Growth of Azotobacter indicum *with Different Sources of Nitrogen.*

Source of N.	log (Turbidity).	Source of N.	log (Turbidity).
N₂ ..	0·245–0·248	Asparagine	0·333–0·382
NaNO₂ ..	0·048–0·057	Aspartic acid	1·32 –(contamin.)
NH₄-lactate ..	0·566–0·642	Glutamic acid	0·800–0·865
Hydroxylamine ..	0·012–0·015	*l*-Leucine	0·600–0·620
Urea ..	0·278–0·292	N, Mo (2·4 p.p.m.)	1·28 –1·40
Glycine ..	0·023–(lost)	Sterile medium	0·020
Alanine ..	0·022–0·022		

20 ml. Mo-free sucrose medium in 250 c.c. round flasks. Incubation 12 days at 32–35° C.

TABLE 12.
Influence of Glycine and Alanine on Growth of

Source of Nitrogen.	...ity).
Free nitrogen ..	1·61 –1·73
Glycine, 80 p.p.m. N ..	0·822–1·17
„ 400 „ „ ..	0·036–0·038
Alanine, 80 „ „ ..	1·37 –1·57
„ 400 „ „ ..	0·038–0·042
Sterile medium ..	0·022

25 ml. sucrose-medium, ... Na₂MoO₄, in 250 c.c. Erlenmeyer flasks. Incubation ... 33° C.

more remarkable that glycine and alanine are not merely non-assimilable, but cause actual inhibition; however, a similar action of single amino-acids has been observed in other instances (Anderson, 1946).

Another experiment, recorded in Table 12, shows that the inhibitory action of glycine and alanine is also displayed in the presence of molybdenum; the lower concentration of glycine (80 p.p.m. N) also causes a significant partial inhibition.

Hydrogenase Production. It may finally be mentioned that a hydrogenase was found in cell material grown with free nitrogen, but not in cells grown with ammonium lactate or glutamic acid. The hydrogenase formed in sucrose and glycerol media was very active towards methylene blue as a hydrogen acceptor, but not towards nitrate, nitrite, or hydroxylamine. With respect to hydrogenase formation *Az. indicum* thus resembles other species of *Azotobacter* (Phelps and Wilson, 1941; Lee and Wilson, 1943).

Observations on Calcium Requirement of Clostridium Butyricum. Attempts were made to grow *Cl. butyricum* in a calcium-free medium in order to ascertain whether calcium is essential for nitrogen fixation by this organism. The methods and medium were the same as stated in a previous communication (Jensen and Spencer, 1947), except that the calcium carbonate was replaced by a buffer mixture of 5·7 gm. Na_2HPO_4 and 0·3 gm. KH_2PO_4 per litre. The results were not altogether conclusive, because the medium rapidly became so acid (pH 3·9–4·5) that growth ceased and only comparatively small amounts of nitrogen were fixed; higher concentrations of phosphate buffer proved inhibitory. Moreover, the potato-extract concentrate contained a certain amount of calcium and imparted a Ca content of approximately 0·3 p.p.m. to the medium. This content, however, was so low that *Az. chroococcum* was capable of practically no nitrogen fixation, and addition of calcium chloride or purification of the medium with oxalate had no significant influence on the limited amount of nitrogen fixed by *Cl. butyricum*. The results suggest that calcium is not necessary for the anaerobic nitrogen-fixing bacteria, or at least their calcium requirements must be much smaller than that of *Az. chroococcum*.

GENERAL CONCLUSIONS.

Az. indicum obviously resembles the other species of *Azotobacter* in the pronounced activation of the nitrogen-fixing mechanism by small concentrations of molybdenum, and in the formation of a hydrogenase when nitrogen fixation takes place. Certain differences also exist, not only with regard to pH-tolerance, but also in so far as *Az. indicum* is not stimulated by vanadium and is inhibited by organic nitrogen compounds like glycine and alanine. The poor growth with asparagine (in comparison with aspartic acid) and with urea and the apparent toxicity of the two amino-acids might suggest that certain amino-compounds are able to block the nitrogen-fixing enzyme by virtue of a similarity in chemical structure to some key-compound of the fixation process. With regard to the utilization of combined nitrogen, *Az. indicum* resembles *Az. chroococcum* and *vinelandii* in its behaviour towards aspartic and glutamic acid (1944), of which particularly the latter appears to occupy
a   tion (Wilson and Burris, 1947), but it differs in its
growth with urea and asparagine. The remarkable
growth with nitrate, which also seems to have
in other *Azoto*   might conceivably be due to the molybdenum
ing rise to some interme   f nitrate less readily assimilable than the
intermediates formed in the a   olybdenum. This is of course only put
forth as pure hypothesis; it must   future experiments to decide whether all
these phenomena indicate that the   nitrogen fixation takes partly different
routes in *Az. indicum* and in the oth   of *Azotobacter*.

Unlike molybdenum, which is e   ential or stimulatory to all definitely
known types of biological nitrogen fix   *Azotobacter*, the clostridia, the blue-
green algae, and legumes plus root   cteria) calcium is according to the
evidence of the present experiments   ersally necessary for nitrogen-fixing

micro-organisms, a fact in agreement with the opinion of Burk and Burris (1941) that calcium, although essential for *Az. chroococcum* and *vinelandii*, is not needed specifically for the process of nitrogen fixation by these organisms.

SUMMARY.

Azotobacter indicum Starkey and De was found to require molybdenum for nitrogen fixation. The effect appeared to begin at a molybdenum-concentration of 0·001 to 0·0001 parts per million, and to reach its optimum at 0·1 to 1·0 p.p.m. Molybdenum could not be replaced by vanadium.

A favourable effect of calcium on nitrogen fixation could not be detected. If this element is necessary at all, quite infinitesimal amounts seem sufficient for maximum fixation.

Addition of 0·1–0·4% agar to the liquid medium accelerated the nitrogen fixation strongly; starch had a similar but smaller effect. From 15 to 18 mgm. nitrogen were fixed per gm. glucose consumed, and occasional gains of more than 20 mgm. per gm. sucrose were observed.

Growth with nitrate was retarded by 0·05 to 5·0 p.p.m. molybdenum. Nitrate, aspartic acid and glutamic acid appeared to be the best sources of combined nitrogen, followed by *l*-leucine, ammonium lactate, asparagine, and urea, in the order mentioned. Nitrite, hydroxylamine, glycine and alanine had inhibitory effects. A hydrogenase was formed in nitrogen-free media, but not in media with combined nitrogen.

Tentative experiments suggested that *Clostridium butyricum* does not require calcium for nitrogen fixation.

ACKNOWLEDGEMENTS.

REFERENCES.

ANDERSON, C. G., 1946.—An Introduction to Bacteriological Chemistry. 2nd Ed. Edinburgh.

BURK, D., and LINEWEAVER, H., 1931.—The Influence of Calcium and Strontium on the Catalysis of Nitrogen Fixation by *Azotobacter*. *Arch. Mikrobiol.*, 2 : 155-186.

————, ————, and HORNER, C. K., 1934.—The Specific Influence of Acidity on the Mechanism of Nitrogen Fixation by *Azotobacter*. *J. Bact.*, 27 : 325-340.

————, and BURRIS, R. H., 1941.—Biochemical Nitrogen Fixation. *Ann. Rev. Biochem.*, 10 . 587-718.

HORNER, C. K., and BURK, D., 1934.—Magnesium, Calcium and Iron Requirements for Growth of *Azotobacter* in Free and Fixed Nitrogen. *J. Agric. Res.*, 48 : 981-995.

————, ————, ALISON, F. E., and SHERMAN, M. S., 1942.—Nitrogen Fixation by *Azotobacter* as Influenced by Molybdenum and Vanadium. *Ibid.*, 65 : 173-192.

————, and ALLISON, F. E., 1944.—Utilization of Fixed Nitrogen by *Azotobacter* and Influence on Nitrogen Fixation. *J. Bact.*, 47 : 1-14.

JENSEN, H. L., and SPENCER, D., 1947.—The Influence of Molybdenum and Vanadium on Nitrogen Fixation by *Clostridium butyricum* and related Organisms. PROC. LINN. SOC. N.S.W., 72 : 74-86.

KRZEMIENIEWSKA, H., 1910.—Die Einfluss der Mineralbestandteile der Nährlösung auf die Entwicklung des *Azotobacter*. *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math. Nat.*, Ser. B : 376-413.

LEE, S. B., and WILSON, P. W., 1943.—Hydrogenase and Nitrogen Fixation by *Azotobacter*. *J. Biol. Chem.*, 151 : 377-385.

PHELPS, A. S., and WILSON, P. W., 1941.—Occurrence of a Hydrogenase in Nitrogen-fixing Organisms. *Proc. Soc. Exp. Biol.*, 47 : 473-476.

PRODINGER, W., 1940.—Organic Reagents Used in Quantitative Inorganic Analysis. New York.

RIPPEL, A., 1936.—Ueber die Wirkung von geringen Mengen von Agar auf Wachstum und Stickstoffbindung von *Azotobacter* und auf andere mikrobiologische Vorgänge. *Arch. Mikrobiol.*, 7 : 210-234.

STARKEY, R. L., 1939.—The Influence of Reaction upon the Development of an Acid-tolerant *Azotobacter*. *Trans. Third Comm. Int. Soc. Soil Sci.*, A : 142-150.

————, and DE, P. K., 1939.—A New Species of *Azotobacter*. *Soil Sci.*, 47 : 329-343.

WARING, W. S., and WERKMAN, C. H., 1942.—Growth of Bacteria in Iron-free Media. *Arch. Biochem.*, 1 : 303-310.

WILSON, P. W., and BURRIS, R. H., 1947.—The Mechanism of Biological Nitrogen Fixation. *Bact. Rev.*, 11 : 41-73.

EXPLANATION OF PLATE XXIII.

1. Effect of molybdenum and vanadium on nitrogen fixation by *Az. indicum* (cf. Table 1); from left : --Mo; 0·001 p.p.m. Mo; 0·01 p.p.m. Mo; 1·0 p.p.m. Mo; 0·2 p.p.m. V. 2. Growth of *Az indicum* in oxalate-purified glucose medium (cf. Table 4). Left, --Ca; right, 0·1% CaCl₂. 3. Effect of agar on growth of *Az. indicum* in glucose medium incubated 8 days (cf. Table 10). Left, 0·1% agar; right, --agar. (The cultures were poured into wide test tubes and photographed immediately before analysis.) (S. Woodward Smith photos.)

STRONGYLURIS DAVISI, N. SP. (NEMATODA), FROM THE STOMACH OF A LIZARD, *DIPORIPHORA AUSTRALIS*.

By PAUL D. HARWOOD,

(*Communicated by Dr. G. A. M. Heydon.*)

(One Text-figure.)

[Read 29th October, 1947.]

Some time ago I received from the School of Public Health and Tropical Medicine of the University of Sydney, Australia, a vial containing thirteen specimens of *Strongyluris* (12 males and one female), which apparently represent a new species. This material was collected by Mr. Consett Davis, who was later killed in war service in New Guinea. Therefore, it is particularly fitting to name this species in honour of the collector.

STRONGYLURIS DAVISI, n. sp.

Specific Diagnosis.

Strongyluris: Body light brown in preserved material; colour in life not recorded. Cuticle with numerous fine longitudinal striations. Somatic papillae absent. Mouth surrounded by three large equal lips set off from the body by a marked constriction. The inner cuticular spike, which is prominent on the lips of *S. rubra*, could not be discovered in the present material.

Male:

Body fusiform, except for the truncated posterior end. Length 11·25 to 14·5 mm.; width at level of oesophageal bulb 0·57 to 0·66 mm.; maximum width 0·61 to 0·9 mm.; head 90μ wide. Pharynx (including lips) 0·22 to 0·28 mm. long. Distance from cephalic end to caudal end of oesophagus 1·95 to 2·35 mm. Oesophageal bulb 0·25 to 0·37 mm. long by 0·22 to 0·27 mm. wide. Nerve ring 0·5 to 0·6 mm. and excretory pore 1·4 to 1·6 mm. from the cephalic end. Tail spike directed dorsad in available material, about 40μ long. Caudal alae present, but smaller than in some forms; supported by large papillae. This material was not well relaxed at time of preservation, consequently manipulations of specimens for purposes of studying the caudal papillae were not easily carried out. The relative positions of the ten pairs of papillae are shown in Figure 1, which was made from the one specimen that showed the location of at least
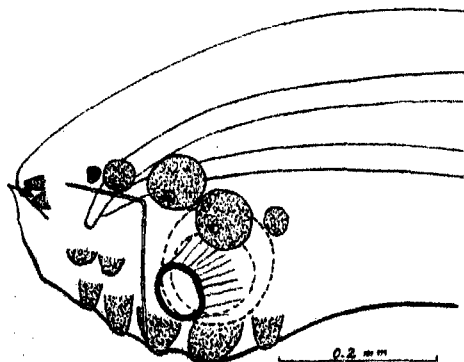
Figure 1.—Tail of male of *Strongyluris davisi*. Latero-ventral view. Only one member of each pair of the adanal papillae could be distinguished. Also only one member of each pair from the most caudal group of papillae is shown because the others are underneath the body of the nematode.

one member of each of the ten pairs of genital papillae. There are three preanal pairs lying close beside the genital sucker; two lateral, stalked, adanal pairs and two more sessile, ventral adanal pairs lying at the level of the cloacal aperture; finally three pairs of small papillae lying near the base of the tail spike. The spicules are 0·86 to 1·13 mm. long. The ratio of the spicule length to the total length varies from as 1 is to 12 to as 1 is to 14. Genital sucker 0·13 to 0·16 mm. in diameter at the base, narrowing to about 0·09 mm. at the aperture. The notch in the caudal rim of the sucker could not be found, possibly due to the condition of the material.

Female:

Body fusiform, length 15·0 mm.; width at oesophageal bulb 0·54 mm.; maximum width 0·69 mm.; head 90μ wide. Pharynx 0·29 mm. long. Distance from the cephalic end to the caudal end of oesophagus 2·25 mm. Lips to excretory pore 0·65 mm. Vulva far posterior, 9·75 mm. from the lips. Tail only 75μ long. Eggs unsegmented, 69μ to 75μ long by 45μ wide; egg-shells thick.

Host: *Diporiphora australis*.

Habitat: Stomach.

Locality: Five Islands, near Wollongong, New South Wales, Australia.

Specimens: Types and paratypes, No. 1135, in the collection of the School of Public Health and Tropical Medicine, Sydney, Australia. Paratypes, No. 45779 in the United States National Museum Helminthological Collection.

Strongyluris davisi keys out to *S. media* in the key to the genus given by Harwood (1935). It may be separated from *S. media* by the slightly longer spicules, the longer oesophagus, and the less prominent caudal alae, which is the clearest difference. The females of *S. davisi* possess a shorter tail and the vulva is nearer the posterior end than with *S. media*.

Among the more recently described species, several possess somatic papillae which clearly distinguish them from *S. davisi*. Others, such as *S. ranae*, *S. bengalensis*, and *S. karawirensis*, have much shorter spicules. *S. tridentata* is larger, has longer spicules, and the most cephalic pair of the caudal papillae are much larger, being at least 348μ by 275μ in *S. tridentata* but only 35μ in diameter in *S. davisi*. *S. meridionalis* is distinguished from the present species by the position of the caudal papillae, the longer oesophagus, and the longer female tail in the former species.

REFERENCE.

HARWOOD, P. D., 1935.—Notes on Tennessee Helminths, II. Two new species of Strongyluris (Nematoda) and notes on the genus. *Jour. Tennessee Acad. Sci.*, 10 : 131-138.

AUSTRALASIAN CERATOPOGONIDAE (DIPTERA, NEMATOCERA).

PART I. RELATION TO DISEASE, BIOLOGY, GENERAL CHARACTERS AND GENERIC CLASSIFICATION
OF THE FAMILY, WITH A NOTE ON THE GENUS CERATOPOGON.

By DAVID J. LEE, B.Sc.

(With 23 Text-figures.)

[Read 29th October, 1947.]

Contents.

The present paper is the first of a series designed to revise and extend our knowledge of Australasian Ceratopogonidae. As some sections of this work have been complete for some time and others have been delayed by extensive additions to the basic material, it has been decided to present the revision in a series of parts, each of which is to be as complete as available material and data permit.

INTRODUCTION.

In common with other blood-sucking insects the Ceratopogonidae have at times come under suspicion as vectors of disease. The earliest such suggestions in Australian literature concern worm nodule in cattle, caused by the filarial worm *Onchocerca gibsoni*. Cleland, Dodd and Ferguson (1916) mention *Culicoides molestus* as being numerous on Milson Island in the Hawkesbury River (New South Wales), whereon they conducted their experiments, and although they record this species as often swarming about the ears of cattle, they discount the possibility of its being the vector. Similarly Dickinson and Hill (1916) list *Culicoides subnitidus* (now *Forcipomyia subnitida*, but this is not likely to have been a correct determination) as one of the biting flies taken in the vicinity of their laboratory at Fanny Bay (Northern Territory), but again do not attach any significance to this finding. There is now, of course, far more reason to suspect a ceratopogonid as the vector of *Onchocerca gibsoni*, since Steward (1933) has shown *Culicoides nubeculosus* to be the vector of *Onchocerca cervicalis* of horses in England, and more recently Buckley (1938) has produced evidence that certain species of *Culicoides* are the vectors of *O. gibsoni* in Malaya. He

Y

found natural infections in *Culicoides* spp. and obtained experimental infections in these insects with a very low percentage of parasitism but was not able to demonstrate actual transmission to cattle.

Elsewhere *Culicoides austeni* and *C. grahami* are known to transmit the filarial parasite *Acanthocheilonema perstans** in Africa (Sharp, 1928), and *C. furens* transmits *Mansonella ozzardi* in South America (Buckley, 1933, 1934).

Apart from their role as vectors of filarias, sandflies† have long been known as irritating and persistent pests of man and domestic animals wherever they may be locally abundant. In Australia this is particularly true of coastal mangrove areas in the vicinity of which the densest sandfly populations are found, but one may be subject to their attacks in a much wider variety of situations. The actual bite is not always noticed by the victim; indeed only particularly susceptible people seem to be immediately aware of the bite, but irritation usually sets in within a few to 24 hours after the time of biting. The irritation may last with decreasing potency for several days, but in some individuals a local toxic condition at the site of the bites may persist for weeks.

When, in 1936, the author was collaborating in experiments designed to discover the vector of ephemeral fever of cattle in Australia, sandflies came under suspicion.‡

Just prior to the outbreak of war in 1939 the first attempts at experimental transmission through the agency of sandflies were made by Dr. I. M. Mackerras at Canberra, using sandflies collected by the author from cattle in Central Queensland. Unfortunately these had to be discontinued even before satisfactory techniques for handling these small insects could be devised.

However, it was soon clear, in these very preliminary studies, that so little was known of the Ceratopogonidae in Australia that it was practically impossible to identify any specimens collected in the field, that not a single life history was known and very little was known of the distribution or habits of any Australian species. In 1936 some preliminary studies of the taxonomy of this group were carried out, together with field observations in the vicinity of Sydney and in Central Queensland. It was soon clear that this particular family of flies was far more common than was previously suspected, and that even in areas where they were not known to occur, even by the local inhabitants, they might still be found in large numbers feeding on cattle. These preliminary studies had then to be broken off and it was not until 1946 that the author was able to give some further attention to this group, the results of which are presented below.

ACKNOWLEDGEMENTS.

---

* Recent texts on Tropical Diseases mention *A. perstans* as occurring, or possibly occurring, in New Guinea. The only evidence for such a statement appears to be a record published by Manson in 1892 which has not been verified or corroborated by later observations. Whether or not the record is true must remain in doubt at present, but the evidence is obviously very slender. Actually, Manson in 1900 (Tropical Diseases, first edition), stated that he had never found *F. perstans* outside of Tropical West Africa and in aborigines of Demarara, but that he had found a microfilaria closely resembling *F. demarquati* in the blood of natives of New Guinea. Now of course *F. demarquati* is regarded as a synonym of *M. ozzardi*. All that can now be said is that an unsheathed microfilaria has been found in natives of New Guinea which has not yet been adequately identified.

† The term sandfly is used in Australia for, both Ceratopogonidae and Simuliidae. Here, of course, only the former are referred to by this term. Further confusion is likely to arise with the sandflies of the Middle East, which are Psychodidae of the genus *Phlebotomus*.

‡ The evidence which may be offered implicating Ceratopogonidae in the transmission of ephemeral fever has been reviewed by Mackerras and Mackerras (1940, p. 108) and Seddon (1938).

§ Most of the material examined, including type series, has been lodged in the Museum of this Institution, which is referred to as the C.S.I.R. Museum in later parts of this series.

Tasmania and the Australian Capital Territory, it would not have been feasible to initiate this present revision.

Other material has been supplied by the School of Public Health and Tropical Medicine, University of Sydney, and I would also like to express my particular gratitude to Messrs. R. H. Wharton, who has assisted me in collecting a large amount of material, J. Henry, who has collected a valuable series of specimens in the vicinity of Sydney, and M. M. H. Wallace, who has provided useful material from both New Guinea and Western Australia. Throughout the series will appear numerous photographs of wings, the excellence of which is due entirely to the skill of Mr. E. Parrish, of the C.S.I.R. McMaster Laboratory, University of Sydney. The co-operation of Mr. Parrish was made possible through the kind offices of Mr. D. A. Gill, Officer-in-Charge, McMaster Laboratory, and Dr. A. J. Nicholson, Chief, Division of Economic Entomology, C.S.I.R., Canberra.

THE FAMILY CERATOPOGONIDAE.
Family Status.

Most authorities have regarded the Ceratopogonidae as merely a subfamily of the Chironomidae, but following Malloch (1917) and Edwards (1926) it is considered that full family status should be accorded to the group. A tabulation of differential characters between the Chironomidae and the Ceratopogonidae is to be found in Edwards (1926).

General Characters of the Ceratopogonidae.

Members of the family Ceratopogonidae are differentiated from those of other families of nematocerous diptera by their small to minute size and compact body with relatively short, strong legs, wings of the same length as the abdomen, prominent chitinized mouthparts extending as a piercing organ ventrally from the head and approximately equal to the height of the head in length and antennae usually as long as or longer than the thorax. The resting attitude is such that the long axis of the head (continuing the line of the mouthparts) is almost at right angles to the long axis of the body and the wings are folded flat over the body, the one lying on top of the other.

Recognition in the field depends to some extent on an appreciation of the characters mentioned above but is, of course, considerably simplified when most of the other groups of small nematocerous flies can be eliminated by immediate recognition. With some practice the general appearance of sandflies may be appreciated to the extent that very little confusion occurs in their field collection, a few Mycetophilidae, small species of Chironomidae and occasional small Phoridae being all that may be mistakenly collected.

Identification under the microscope is relatively simple with Australasian species, since they are the only flies in which all branches of the reduced radius meet the costa before the apex of the wing and usually about the centre of the anterior margin, enclosing one or two radial cells, with both M_1 and M_2 present and the $M_{3+4} - Cu_1$ fork near the middle of the wing. These wing characters, in conjunction with the shape of the antennae, which are moderately long with from the last one to the last six obviously longer than the basal flagellar segments and the chitinized piercing mouthparts, serve to distinguish the group.

It is at present rather more difficult to characterize the larvae of the Cerato-pogonidae, since there are a number of distinct types. However, in all except the Leptoconops group there is a distinct chitinized head capsule and the thorax is differentiated into three segments. In most the body tapers distinctly to both ends and some are apparently smooth without any obvious external structures and others have lateral and/or dorsal chitinous prolongations or setae. Some have a pair of prothoracic prolegs and a pair of posterior prolegs (on anal segment), others only a posterior pseudopodium. The majority of larval forms fall within these types which will be found defined in more detail below.

Less difficulty should be occasioned in the recognition of the pupae. These are obviously divided into a cephalothoracic region and a segmented abdomen, both regions being strongly chitinized. The paired breathing horns arise laterally at or near the anterior end, and on the abdominal segments there are strongly chitinized angles or prolongations laterally, and the terminal segment has a pointed prolongation on each postero-lateral angle. The pupae are capable of restricted movement only and may be free from the larval exuvium or with the latter surrounding the distal portion of the body.

Habits.

Although the most commonly known species are those whose adult females suck the blood of man, others attack other vertebrates. *Culicoides* and *Leptoconops* and related genera are particularly well known for their anthropophilic species. Other groups are recorded as sucking a wide variety of insects such as Chironomidae, Culicidae, Lepidoptera and Coleoptera and even other Ceratopogonidae. One genus, *Pterobosca*, has only been taken from the wings of Odonata. Kieffer (1925) also mentions that large numbers of adults, almost invariably females, may at times be taken from the flowers of various Umbelliferae.

Blood-sucking adults may be collected by exposing oneself to attack under suitable conditions. Sandflies are known to bite at almost any time of the day (some are recorded as nocturnal), particularly when there is a very dense population of these insects. Where they are not present in large numbers a combination of warm moist conditions without wind will often disclose them biting in the very early morning or late afternoon. Animals such as cattle, horses or dogs may often attract species which pay little attention to humans. Predatory species may be collected by sweeping vegetation with a fine net in areas adjacent to probable breeding sites (pools, streams and so on) or by picking them from the vegetation individually once one has learnt to distinguish their general shape from other types of small Diptera. Large numbers of sandflies are at times attracted to lights in bush areas and this has proved a useful method for collecting species of *Forcipomyia*.

Nothing has yet been published concerning the larvae of Australian species. Searches by the author in mangrove areas have as yet failed to yield any Ceratopogonid larvae or pupae but both stages of several species (of *Culicoides* and *Dasyhelea*) have commonly been found in small rock pools in both coastal and mountain streams in the Sydney district and in rather similar situations in Central Queensland.

Elsewhere in the world the recorded larval habitats are very various, ranging from wet sand between tide levels through wet, muddy areas to pools in streams, the margins of small lakes, dams and so on, often in blanket or filamentous algae; in tree holes; and also in moist decaying vegetation; under the bark of trees and even in the exudate from wounds in the holes of trees such as maple and elm. A few species have also been recorded in the nests of ants. Obviously, then, much has still to be discovered concerning the life histories of Australian species.

DETAILED CHARACTERS OF THE FAMILY.

Although the present series is to be largely devoted to the systematics of the Ceratopogonidae, with particular reference to adults, brief characterization of eggs, larvae, and pupae have been included to assist any new student of the group in recognizing these stages.

Eggs.

These have not been seen by the author, but they may resemble those of the Chironomidae in being laid in masses, some in long ribbons, others in compact groups. Other species are recorded as ovipositing singly. The individual eggs are elongate and cylindrical, usually straight, but those of *Dasyhelea* are horseshoe-shaped.

Larvae.

The following information is a condensation of that contained in Goetghebuer (1920), Kieffer (1925) and Thomsen (1937). There is general agreement that there

are three recognizable forms assumed by the larvae which correspond to three corresponding pupal forms and to a lesser extent to adult groupings.

The first grouping is that in which the larvae possess a pair of anterior prolegs ventrally on the prothorax and another pair of posterior prolegs on the anal segment. The body is not vermiform but has the dorsal surface covered with at least short setae which may be modified into variously formed appendages. The mandibles are directed ventrally. This group comprises the larvae of *Forcipomyia, Atrichopogon* and closely related genera.

In the second group no anterior prolegs are present but there is, however, a retractile anal pseudopodium. The body is vermiform and lacks any distinct setae or modified structures. The mandibles are also directed ventrally. To this group belong the larvae of *Dasyhelea.*

The third group lacks all prolegs or pseudopodia, the body is also vermiform, without appendages, and the mandibles in this case are forwardly directed. Members of this group comprise *Culicoides* and the *Palpomyia, Stilobezzia* and *Bezzia* groups of genera.

In addition, however, a fourth grouping must be contemplated to include the larvae of *Leptoconops* and its allies, about which very little is yet known. Thomsen (1937) indicates that prothoracic prolegs are lacking and that "the head is not sclerotized, but provided with a system of heavily sclerotized rods and levers", this information coming from Painter (1926).

Pupae.

The general appearance of the pupae has been detailed above. Three groups of pupal forms are to be correlated with the first three larval groups mentioned above.

Those of the first larval group (*Forcipomyia, Atrichopogon* and related genera) have the thoracic trumpets usually arising from a stalk and swollen distally with a sinuous distal margin bearing the spiracular openings or else the trumpet rather strongly resembles an ear. The posterior portion of the abdomen is held within the cast larval skin.

Species of the second group (*Dasyhelea*) and also the third have the pupae free of the larval exuvium but may be differentiated by the form of the posterior border of the apical segment (between the spines). In the second group a pair of small tubercles from which a minute hair arises is found on this margin, whereas species of the *Palpomyia, Culicoides, Bezzia* and *Stilobezzia* groups lack these structures.

Adults.

A number of papers on the Ceratopogonidae [viz., Carter, Ingram and Macfie (1920), Goetghebuer (1920), and Kieffer (1925)] include fairly detailed accounts of the anatomy of these flies and also include many useful explanatory figures. The following account emphasizes the characters found most useful in a study of Australasian species, but an attempt has also been made to indicate the differential characters of other groups not as yet found in the Australasian region.

Size: The variation in size is rather wider than one only accustomed to the small anthropophilic species would imagine, and in known Australian species there is a range of body length (head to tip of abdomen) of from about 1·0 mm. to 3·5 mm. and in wing length from 0·8 mm. to almost 4·5 mm.

Head: The head is subglobular, the anterior face being rather characteristically flattened, and this appearance is emphasized by the anterior surface being in line with the dorsal surface of the elongated mouthparts, the length of which is roughly equivalent to the height of the head and rarely only about one-fourth the height of the head. The dorsal surface of the head, comprising the posterior occiput and undifferentiated anterior vertex, is invested with scattered setae and a row of orbital bristles overhang the eyes. The eyes may be joined or separated by an inter-orbital space and, if separate, they are usually more widely spaced in the male than in the female. Some genera, e.g., *Atrichopogon* and *Stilobezzia*, appear to be characteristically

holoptic, and others, e.g., *Culicoides* and *Palpomyia*, usually have the eyes separated. In *Culicoides* the narrow inter-orbital area in the female bears a single strong seta just below the vertex (Text-figure 12), and this character may be useful in placing species whose generic position may be difficult to establish otherwise. In *Leptoconops* (sens. lat.) the eyes are far more widely separated than in any other group. The eyes themselves are usually bare but may be finely pubescent between the facets (as in *Dasyhelea*).

The antennae (Text-figure 12) comprise fifteen segments in most genera (a reduction to from twelve to fourteen segments occurs in *Leptoconops* and related genera), the first being usually reduced to a ring-like segment around the base of the enlarged second segment or pedicel, but in females of *Culicoides* the first segment may be almost as large as the second. The pedicels of the female are separated but in the male they are further enlarged and often touching. The flagellum then comprises thirteen segments, but the shape of the individual segments varies in different genera and furnishes useful diagnostic characters. The first eight flagellar segments of the female vary from transverse to cylindrical but are nearly always markedly shorter than the last five (or six in *Pterobosca*). In males usually the last four flagellar segments are elongated. (In the *Leptoconops* group of genera the antennae are somewhat similar to those of the *Simuliidae*, with very short flagellar segments, and in this group only the apical segment is elongated. See Text-figure 14.) There are sparse verticels on the flagellar segments of the female (usually reduced on the distal, differentiated segments) and the male has dense, applied verticels of very long hairs on the second to tenth flagellar segments. Occasionally, as in *Atrichopogon* the terminal antennal segment ends in a small stylet and in most species of *Dasyhelea* the integument of the antennal segments is sculptured (see Text-figure 17).

The mouthparts of the female are composed of seven distinct parts, the strong, apically toothed labrum, the paired maxillae and mandibles, both slender structures with distal serrations, those of the maxillae being by far the most obvious; the tubular hypopharynx and the enclosing sheath or labium, which is hairy externally. In the male the mouthparts are somewhat shorter, the labium similar but narrower, and the other parts neither as strong nor as powerfully armed. The palpi are normally of five segments (reduced to four in *Leptoconops*) and of these the second and third are longer than the rest, and the third is often expanded distally around a sensory area.

Thorax: The thorax is rather squat, scarcely longer than broad, broadest anteriorly but not narrowing greatly until just before the scutellum. The anterior end is strongly arched but does not project over the head, and the prescutellar area is well marked as a flattened or lightly depressed, anteriorly rounded, laterally and posteriorly straight area. There may also be a pair of humeral pits (Text-figure 23) laterally near the anterior margin (*Culicoides*, *Stilobezzia*) or at the middle of the anterior margin a small spine may arise (*Palpomyia*). The surface of the scutum is variously adorned in different genera, sometimes it is glabrous, in others there is a distinct pattern resulting from the surface bloom (pruinescence). There may be a uniform covering of minute, pubescent hairs or there may be longitudinal rows of short setae. The pleura vary in the shape of the pleurites, the extent of chitinization of the anepisternum and the development of the meron, the variations being correlated with major divisions of the family (see below, page 324). Text-figures 1 and 2 illustrate the form of the thorax, in lateral view, as found in *Atrichopogon* and *Xenohelea*.

Legs: The legs are shorter and more thickset than in the Chironomidae. Many features of diagnostic importance are to be found in the legs, including the size of the femora (they may be considerably swollen in some species) and the presence or absence of spines on them, the ratios of the length of various segments, particularly those of the tarsi, the presence or absence of spines on the tarsal segments, the shape of the tarsal segments, particularly the fourth and fifth, the size and shape of the claws and the presence or absence of an empodium. It is sometimes important to differentiate between what are usually called spinules, that is rather thick black, but tapering spines, and the stouter, blunt, non-tapering "batonnets".

Scutum

Anterior spiracle

Posterior pronotum
Pronotal lobe
Membranous
    anepisternum

Propleuron

Coxa I

Sternopleuron

Coxa II

Wing base
Scutellum
Haltere
Postnotum

Posterior spiracle
Mesepimeron
Meron
Coxa III

1

Paratergite

Chitinous anepisternum

Meron

2

Sternopleuron

Costa R_1
Subcosta R_{2+3}
Radius   First radial cell   Second radial cell
Media R_{4+5}
        Intercalary fork
Anal M_1
3 M_2
Cu_2 M_{3+4}
Cu_1 r-m

Text-figures 1-3.—Text-figure 1. Lateral view of thorax of *Atrichopogon* sp. Text-figure 2. Lateral view of thorax of *Xenohelea* sp., with parts showing striking differences from *Atrichopogon* labelled. In both text-figures 1 and 2 membranous areas of the pleura are stippled. Text-figure 3. Wing of *Stilobezzia* sp. showing terminology of venation. Various magnifications.

Wings: Although the wings are particularly important in generic segregations, much confusion is caused by the various nomenclatures adopted for the venation. Text-figure 3 reveals the terminology used in this series following the Comstock-Needham system as interpreted for Nematocera by Tillyard, and Table 1 gives the corresponding

TABLE 1.

Wing Venation.

Symbol and Name Used in this Series.	Name Used by Kieffer.	Name Used by Skuse.
C. Costa.	Costal vein.	Costa.
Sc. Subcosta.	Subcostal vein.	Auxiliary.
R_1 Radius 1.	Radial vein.	First longitudinal.
R_{2+3} Radius 2 and 3.	—	Marginal cross-vein.
R_{4+5} Radius 4 and 5.	Cubital vein.	Second longitudinal.
r-m. Radio-median cross-vein.	Transversal.	Middle cross-vein.
Intercalary fork.	Intercalary fork.	Third longitudinal.
M_1. Media 1.	Anterior branch of discoidal vein.	Anterior branch of fourth longitudinal.
M_2. Media 2.	Posterior branch of discoidal vein.	Posterior branch of fourth longitudinal.
M_{3+4}. Media 3 and 4.	Anterior branch of postical vein.	Anterior branch of fifth longitudinal.
Cu_1. Cubitus 1.	Posterior branch of postical vein.	Posterior branch of fifth longitudinal.
Cu_2. Cubitus 2.	—	—
An. Anal.	Anal.	

terminologies used by Skuse and Kieffer, the two major authors on Australian Ceratopogonidae. The outstanding features of the venation are the reduction of the radius and the termination of all its extant branches in the costa and the union of the radius to the media by a cross vein (except in *Leptoconops* and its allies). Points of particular importance concerning the venation are the length of the costa, the number of cells formed by the branches of the radius and the costa (one or two), the relative size of these radial cells, and the position of the base of M_2 in relation to the r-m cross vein. Sometimes a fork, the intercalary fork, is seen in the antero-distal section of the wing. Both microtrichia and macrotrichia may or may not be present on the wing membrane, and in some species the wings are densely clothed with recumbent, almost scale-like long hairs. In some species (particularly of *Culicoides*) the wings are spotted, this appearance being most marked when the wings are viewed by oblique lighting.

Abdomen: The abdomen is usually short and broad and blunt, but even if somewhat elongate, does not obviously exceed the length of the wings. The female abdomen terminates in a pair of short, rounded or pointed lamellae in most genera (they are excessively long in *Leptoconops*). The number and shape of the spermathecae are at times useful in classification.

Male Genitalia: These are simple, with, usually, the ninth tergite a large plate superimposed over the majority of the rest of the structures, and its internal and apical surfaces may be considerably modified. The coxites are simple, without accessory structures, except the terminal style, which is also usually simple. The harpes are paired sub-median structures (sometimes fused), which may be useful in specific diagnosis, and there is a median phallosome shaped like an inverted Y and there may be modifications at its distal extremity (the base of the Y). Rotation of the terminalia may be complete or incomplete.

GENERAL SYSTEMATICS.

Previous Australian Literature.

Although over eighty species of Ceratopogonidae have been described or recorded from the Australasian Region (Australia, New Guinea and the Bismarck Archipelago, and New Zealand, other Pacific islands being excluded from the total) the problems of identification have remained extremely difficult. Many of these species were not described in the genera to which they would now be assigned. Many new genera have been defined since 1889, when Skuse described some seventeen species, all of which, with the exception of one, he placed in the genus *Ceratopogon*. Furthermore, Skuse ignored a number of generic names which were available at that time. Changes in generic concepts have also taken place even since Kieffer's description of a further twenty-five species in 1917. Since the latter date no one has paid any particular attention to this family in Australia except Carter (1921), who revised the genus *Leptoconops*, and Macfie (1939*b*), who revised the status of six species. Descriptions of individual species have been published from time to time by various authors, namely, Schiner (1868), Taylor (1911, 1918), de Meijere (1915, 1917) and Macfie (1939*a*). In recent years attention has been paid to New Zealand species by Ingram and Macfie (1931*a*) and Macfie (1932). Apart from *Leptoconops* nothing approaching a revision of even a single genus has previously been attempted.

Difficulties in Recognizing Genera.

The difficulties in working with this group are initially at the generic level. Kieffer's "Key for the Determination of Genera" (1926) separates some 59 genera and Macfie's "Key to Genera" (1940) separates 63 genera. However, 21 of the genera mentioned by Kieffer apparently fall into synonymy when revised by Macfie, and 24 of the genera listed by Macfie are not mentioned in Kieffer's key. This is clearly indicative of the state of flux of generic conceptions. A further difficulty arises in that many genera have not been adequately defined, although Edwards' (1926) revision of British species contains reasonably full generic diagnoses of the genera occurring in Great Britain. The absence of full generic definitions in Macfie's (1940) key to genera detracts from the usefulness of this work, although it is of value as a concise statement of his findings after many years of work with this group.

Naturally, when one tries to identify an Australian specimen generically, according to Kieffer's 1926 key, or Edwards' generic definitions of 1926, or yet again Macfie's 1940 key, the results from each attempt are not always in agreement. This is partly due to the fact that present generic distinctions are often artificial and based on trivial rather than fundamental characters. It does seem agreed that a comprehensive study of male genitalia characters would lead to a more natural and workable grouping of species, but this is a project for which much special collecting would be necessary in all zoogeographical regions. It does appear to the author, and there is some evidence that in the opinion of Edwards also, that the number of genera might be reduced considerably if they are to delimit reasonably natural groups. The adoption of some of the present genera as subgenera would certainly lend clarity to the systematics of the group, but any generic revision is undoubtedly the province of a worker with access to far more material than the present author.

In the following review, apart from the description of newly discovered species an attempt is made to identify generically all described species from Australia, New Zealand and New Guinea as well as to disclose the characters by which individual species may be recognized. When doubt arises as to what genus a particular species belongs an attempt is made to place it with the species to which it appears most closely related and about whose generic status there appears less doubt. A perusal of the literature reveals that more than one author has in the past been forced to place species in genera into the circumscription of which they do not really fit, but to which they appear to belong because of their apparently obvious relation to other species legitimately placed in such genera. Even Ingram and Macfie (1931*b*, p. 215) have had

TABLE 2.

Differentiation of the Ceratopogonidae into Groups on Characters found in the Larvae, Pupae and Male Genitalia.

Group Culicoides.	Group Ceratopogon.	Group Stilobezzia.	Group Macropeza.	Group Palpomyia.	Group Bezzia.
Present.	Not known to be present.	Present.	Not known to be present.	Present.	Present.
Culicoides.	------	Stilobezzia, Acantho-helea, Monohelea.	--- ---	Palpomyia, Clinohelea, Heteromyia, Xeno-helea, Johannsen-omyia, Dicrohelea.	Bezzia, Nilobezzia.
Head capsule present; wide, oval; mouthparts reduced; anterior and posterior pro-legs absent; last segment with bristles; body slender, round in cross - section; pharyngeal skeleton with about four combs, angulus of distinctly separate parts.	Not adequately known. In genus Alluaudomyia head capsule present; anterior and posterior prolegs absent; last segment with long setae; body slender, round in cross - section; dorsal surface mottled with red pigment.	Head capsule present, broad; mouthparts reduced; anterior and posterior pro-legs absent; last segment with bristles; body curved, round in cross - section; pharyngeal skeleton with several combs, principal comb of angulus undivided.	Not adequately known.	Head capsule present; narrow; mouthparts reduced; anterior and posterior prolegs absent; last segment with bristles; body round in cross-section; pharyngeal skeleton, with three combs, principal comb of angulus divided.	As for Palpomyia.
Free from larval exuviae; respiratory trumpet elongate, tubular with a constriction at base; segments 3-7 similarly bristled; anal segment without a bristle-tubercle.	Not adequately known. In Allu-audomyia free from larval exuviae; respiratory trumpet funnel - shaped, covered with scales.	As in Culicoides.	Not adequately known.	Free from larval exuviae; respiratory trumpet clavate, with numerous spiracles; segments 3-7 similarly bristled; anal segment with a bristle-tubercle; operculum with one pair of setae.	As for Palpomyia but in known pupae more than one pair of setae on operculum.
Harpes slender and tapering with variously shaped extremities; ninth sternite emarginate; ninth tergite usually with a sharply pointed process at each postero-lateral angle; anal segment membranous with a pair of hairy tubercles which may project beyond the margin of the ninth tergite; phallosome V- or Y-shaped.	Harpes paired, robust, either tapering or ending bluntly.	Harpes paired, robust, blunt or pointed at extremity but not attenuated, fused on mid line in some species of Monohelea.	Not adequately known.	Style simple; harpes fused into a single structure or less commonly distinctly separated, although they may be connected at base.	As for Palpomyia.

TABLE 2.

Differentiation of the Ceratopogonidae into Groups on Characters found in the Larvae, Pupae and Male Genitalia.

	Group Leptoconops.	Group Atrichopogon.	Group Forcipomyia.	Group Dasyhelea.
Occurrence in Australasian Region.	Present.	Present.	Present.	Present.
Genera known to occur in Australasian Region.	Leptoconops, Styloconops.	Atrichopogon.	Forcipomyia, Lasiohelea, Pterobosca, Apelma, ? Thyridomyia.	Dasyhelea.
Larvae.	Head capsule not chitinized; mouth parts reduced; without prolegs or anal bristles; pharyngeal skeleton with apparently only one comb.	Head capsule present; mouth parts well developed; with anterior and posterior prolegs; all body segments with short spines; anal segment with double row of hooks; body flattened, transversely oval in cross-section; lateral processes at least as long as segment; pharyngeal skeleton with about six combs, angulus with bristles.	Head capsule present; mouth parts well developed; with anterior and posterior prolegs; body segments with short spines; body segments circular in cross-section; pharyngeal skeleton with about six combs, angulus with bristles.	Head capsule present, short and thick; mouth parts well developed; anterior prolegs absent, last segment with retractile proleg with 10–12 hooks; body curved; pharyngeal skeleton with about six combs, angulus with well developed teeth.
Pupae.	Segments 3–7 similar; anal segment with tubercles, terminal processes simple; respiratory trumpets elongate, ending in a short ovate or barrel-shaped structure with about 10 spiracles.	With larval exuviae attached to last three segments; respiratory trumpets short, knoblike; abdominal segments with branched or setaceous projections on first five.	Similar to Atrichopogon but with spines or stump-like projections on all but last segment.	Free from larval exuviae; respiratory trumpets elongated; abdominal segments 2–7 similarly bristled; anal segment in addition to the two apical processes with at least one pair of protuberances.
Male genitalia.	Styles apically bifid or trifid. (Imperfectly known.)	Harpes lacking, or perhaps membranous; ninth sternite narrow, posterior margin emarginate; ninth tergite long, posterior margin rounded, usually without notch; phallosome usually about as broad as long, more or less shield-shaped.	Harpes slender, tapering, often attenuated distally, these may be connected anteriorly at the base by a transverse rod or plate. In Apelma the structure is more compact, the distally projecting processes very short. In a few species these processes appear to be lacking, only the transverse bar remaining visible as in some species of Lasiohelea.	Harpes in most cases asymmetrical, ninth sternite in some cases emarginate, more often with a central posterior extension; ninth tergite rather long, tapering, with a finger-like process on each latero-posterior angle; phallosome broad; styles either simple or with a basal branch.

to do this with Patagonian species of *Palpomyia*, and a similar difficulty faced de Meillon (1936, p. 187) also with a species from South Africa placed by him in *Palpomyia*. No excuse seems necessary, then, if a similar procedure is occasionally adopted in this revision.

Divisions of the Family.

Fortunately certain groups of genera are sufficiently discrete to be recognizable with some ease. These groupings were even accorded subfamily rank by Enderlein (1936), who recognized the following subfamilies: Leptoconopinae, Forcipomyinae, Ceratopogoninae, Palpomyiinae and Bezziinae. Macfie (1940) considered that apart from the Leptoconopinae all the other subfamilies are untenable because of the common occurrence of annectant forms between them. Nevertheless some form of grouping is necessary, and whether Enderlein's five subfamilies or the nine groups proposed by Macfie are adopted depends largely on their practicability.

Johannsen (1943) has also subdivided the family in a very similar way to Macfie, but divides one of Macfie's groups into two (*Forcipomyia* into *Atrichopogon* and *Forcipomyia* groups) and combines two of Macfie's groups in one (*Palpomyia* and *Bezzia* groups). For our purposes it seems most suitable to accept the first of these differences from Macfie's division, but to disregard the latter. In this way we have the family divided into ten distinct groups, eight of which are known to occur in the Australasian region. Reference to Table 2 will indicate the genera so far recognized from our region and the groups to which they belong as well as the differential characters of each group as found in the larval and pupal forms, and also in the male genitalia. The more obvious characters of the adults are discussed in the text below.

The groups (named after the principal genus) are as follows: (1) *Leptoconops* group, (2) *Forcipomyia* group, (3) *Atrichopogon* group, (4) *Dasyhelea* group, (5) *Culicoides* group, (6) *Ceratopogon* group, (7) *Stilobezzia* group, (8) *Macropeza* group, (9) *Palpomyia* group, and (10) the *Bezzia* group. The first of these, the *Leptoconops* group, is quite discontinuous from the rest of the family and is obviously deserving of subfamily status, although it is not at present feasible to adopt this status when the splitting of the remainder of the family into groupings of similar status cannot yet be accomplished satisfactorily.

TABLE 3.

Major Divisions of the Ceratopogonidae.

First Division. (*Leptoconops* Group.)	Second Division. (*Forcipomyia*, *Atrichopogon*, *Dasyhelea*, *Culicoides* and *Ceratopogon* Groups.)	Third Division. (*Stilobezzia*, *Macropeza*, *Palpomyia* and *Bezzia* Groups.)
Body short, not hairy.	Body comparatively short and hairy.	Body more slender and much less hairy.
Antennae with 12–14 segments.	Antennae with 15 segments.	Antennae with 15 segments.
Broad, bare wings.	Broad and usually hairy wings.	Narrow, bare wings.
Costa short, radial cells not distinguishable, r-m absent, anal vein straight, anal area large.	Costa often short, second radial cell often reduced in length, r-m present, anal vein straight, anal area large.	Costa reaching well beyond middle of wing, second radial cell long, r-m present, anal vein bent at the middle, anal area often reduced.
Lateral piece of scutum (paratergite) narrow.	Lateral piece of scutum (paratergite) narrow.	Lateral piece of scutum (paratergite) relatively broad.
Unchitinized portion of anepisternum narrow and oblique.	Unchitinized portion of anepisternum large and vertical.	Unchitinized portion of anepisternum narrow and oblique.
Femora and claws unmodified.	Femora and claws unmodified.	Femora, or claws, or both variously modified.
Species attacking man.	Many species attacking man and other vertebrates but some species attack other insects.	All species apparently predatory on other insects. No blood-sucking species.

Edwards (1926) divided the Ceratopogonidae, exclusive of the *Leptoconops* group, into two main groups, which he distinguished on a number of characters, a consideration of which is undoubtedly of assistance when attempts to sort specimens are made with the limited data available in Macfie's key to groups (1940, p. 13). Adding the *Leptoconops* group as a separate division, Edwards' division would be roughly as detailed in Table 3.

<div align="center">FIRST DIVISION.</div>

<div align="center">*Leptoconops Group.*</div>

This is a compact group in which four genera are recognized by Macfie but only two of these are known to occur in the Australasian region. They are primarily differentiated from all other Ceratopogonids by the absence of the r-m cross vein and the reduction of the antennal segments in the female to from twelve to fourteen. The appearance of the antennae with the majority of the flagellar segments short and broad and only the apical one differentiated is reminiscent of the Simuliidae, but the wing venation is distinctive. All branches of the radius fuse in such a way that there are no distinct radial cells and the radius terminates at or before the middle of the wing. Between the radius and the media is found a vein-like thickening extending from the base of the wing to the distal margin* (see Text-figure 4). *Leptoconops* and *Styloconops* are the two genera known to occur in our region.

(*All other Ceratopogonidae have the r-m cross vein present and the female antennae have fifteen segments.†*)

<div align="center">SECOND DIVISION.</div>

<div align="center">*Forcipomyia Group.*</div>

The presence of a well-developed empodium between the claws of both sexes (in the female only in *Apelma*) distinguishes both the *Forcipomyia* and *Atrichopogon* groups from all the other Ceratopogonids.

In the *Forcipomyia* group there are abundant macrotrichia covering the greater part of the wing. These are recumbent and often scale-like. The radius terminates at about the middle of the wing and the first radial cell is very narrow and often obliterated. The scutum is generally hairy all over. The genus *Lasiohelea* is included in this group although it is in some respects intermediate between *Forcipomyia* and *Atrichopogon*, but the appearance of the wings is such that confusion with *Atrichopogon* is unlikely. Of the genera included in this group, *Forcipomyia*, *Lasiohelea*, *Apelma* and *Pterobosca* have been definitely recognized in the Australasian region. Other genera may still be found, in particular perhaps *Thyridomyia* and *Lepidohelea*.

<div align="center">*Atrichopogon Group.*</div>

This group comprises species in which the macrotrichia of the wings are comparatively sparse and suberect with the radius extending beyond the middle of the wing, usually to about two-thirds from the base and with both radial cells distinct, the second being two or more times the length of the first (see Text-figure 6). The scutum is bare, or with only short fine hairs.

(*All the remaining groups have the empodium rudimentary and inconspicuous.*)

<div align="center">*Dasyhelea Group.*</div>

In the wings of members of this group the first radial cell is more or less obliterated, the second, if open, is oblong or square, and R_{4+5} is characteristically square-ended or at least sharply angled at the end, and terminates at about the middle of the wing (see Text-figure 8). Macrotrichia are present, sometimes covering the greater part of the wing, sometimes restricted to the distal portion, but in most

---

* The interpretation of the venation is discussed in greater detail in Part II of this series.
† Occasional reductions in number of antennal segments have been recorded—e.g., *Lasiohelea natalia* de Meillon has eleven segments in the female antennae and fifteen in the male.

species macrotrichia are characteristically absent for a short distance on either side of all wing veins (see Text-figure 8).
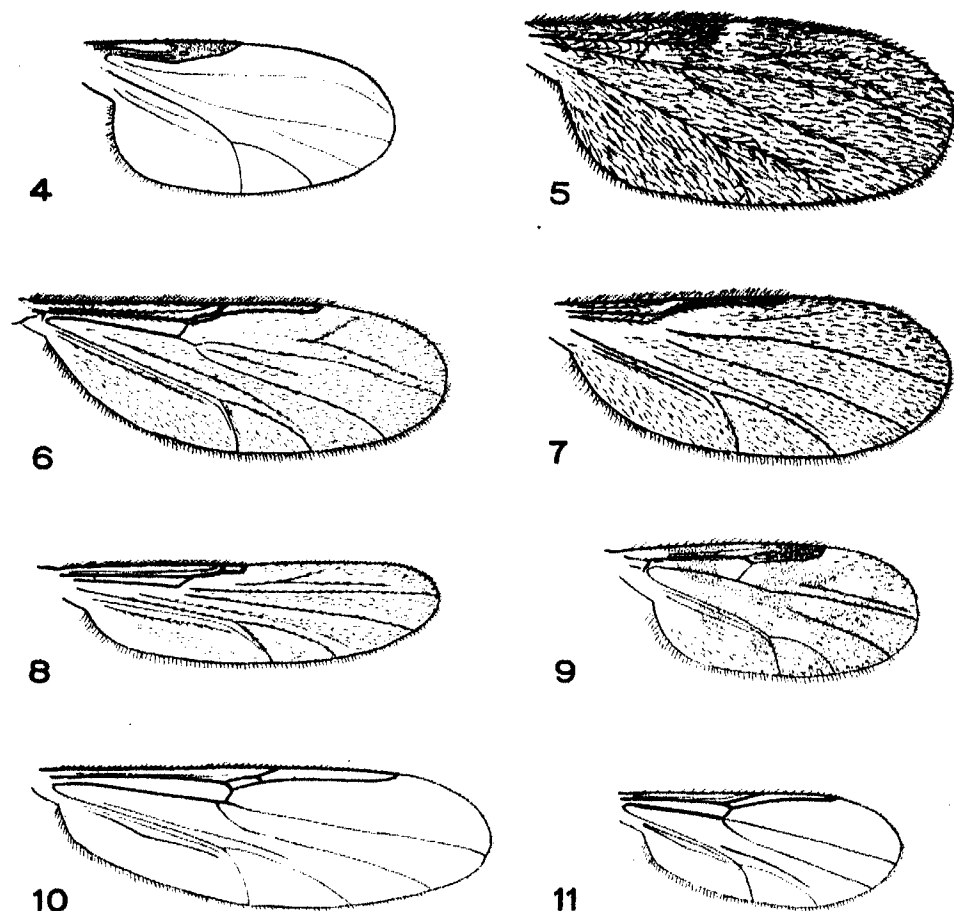
Text-figures 4-11.—Typical wings of various genera. Text-figure 4. *Styloconops*. Text-figure 5. *Forcipomyia*. Text-figure 6. *Atrichopogon*. Text-figure 7. *Lasiohelea*. Text-figure 8. *Dasyhelea*. Text-figure 9. *Culicoides*. Text-figure 10. *Palpomyia*. Text-figure 11. *Bezzia*. (For *Stilobezzia* see Text-figure 3.)   Various magnifications.

Culicoides Group.

Most species of this group have spotted wings (Text-figure 9), a feature not commonly found in other groups. Usually both radial cells are distinct and subequal, and R_{4+5} terminates at or beyond the middle of the wing, but usually before the level of the end of Cu_1. Microtrichia are distinct and macrotrichia are present, even if only at the apex of the wing. A pair of humeral pits are present anteriorly on the scutum (Text-figure 23). The female claws are equal and small (Text-figure 19).

Ceratopogon Group.

This group is closest to Culicoides. Microtrichia may be present or absent, but if macrotrichia are present they are restricted to the wing tip. The two radial cells are small and subequal and R_{4+5} terminates beyond, but not far beyond, the middle of the wing. Humeral pits are usually distinct and the tarsal claws are large but may be equal or unequal. For further details concerning this group see below (page 329).

THIRD DIVISION.

The members of this division are in the main large species on the wings of which macrotrichia are absent or sparse, the radial veins are clearly defined and R_{4+5} terminates well beyond the middle of the wing. The body is relatively free of hairs and there are modifications in the form of spines, unusual shape or enlargement of the femora, tarsi or claws.

Stilobezzia Group.

In this group the median fork is always petiolate (Text-figure 3), a feature which distinguishes it from all the succeeding groups. There are usually two
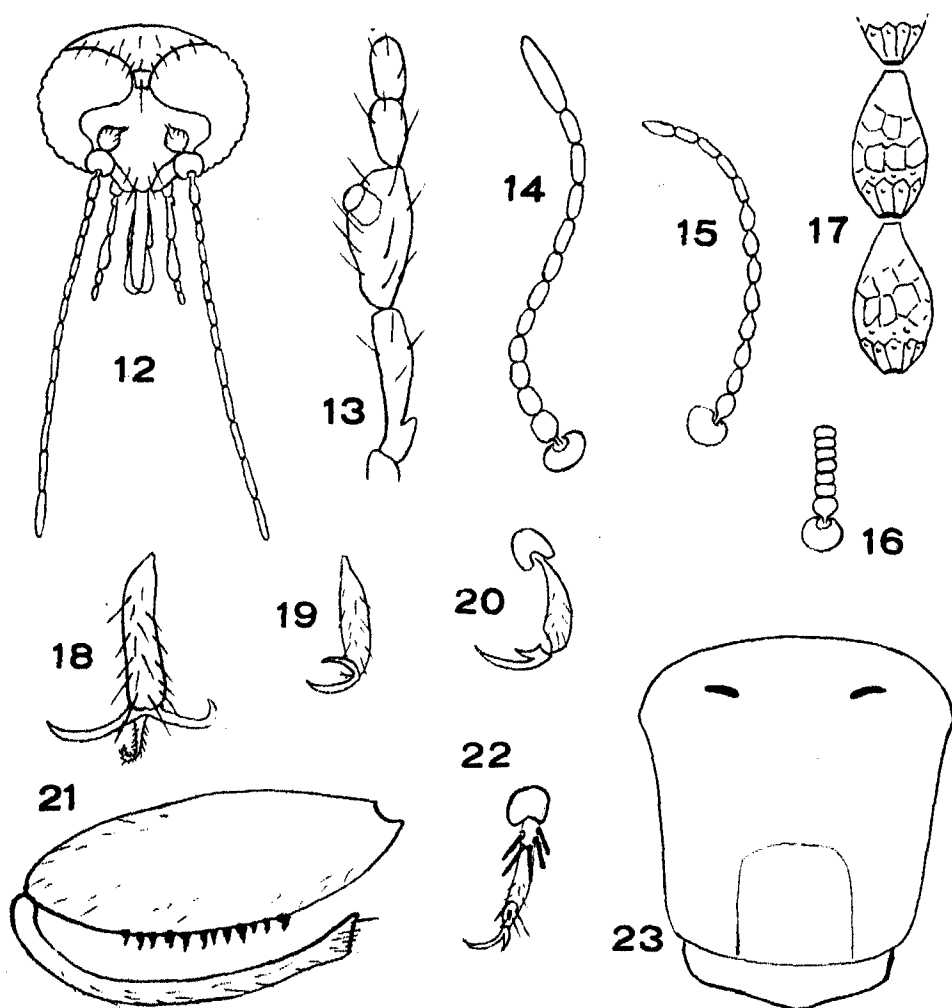
Text-figures 12-23.—Various structures mentioned in the key to genera. Text-figure 12. Anterior view of head of *Culicoides*. Text-figure 13. Enlarged palpus of *Culicoides*. Text-figure 14. Antennal segments 2-14 of *Leptoconops*. Text-figure 15. Antennal segments 2-15 of *Forcipomyia*. Text-figure 16. Transverse basal antennal segments of *Apelma*. Text-figure 17. Sculpturing on antennal segments of *Dasyhelea*. Text-figure 18. Fifth tarsal segment of *Forcipomyia* showing empodium. Text-figure 19. Fifth tarsal segment of *Culicoides* showing hair-like empodium. Text-figure 20. Fourth and fifth tarsal segments of *Stilobezzia*. Text-figure 21. Anterior femur and tibia of *Heteromyia*. Text-figure 22. Fourth and fifth tarsal segments of *Xenohelea*. Text-figure 23. Dorsal view of thorax of *Culicoides* showing humeral pits. Various magnifications.

well-defined radial cells, of which the second is considerably longer than the first. Macrotrichia may be present on the distal portion of the wing and an intercalary fork is usually distinguishable. Modifications of the legs are various in the different genera of the group. The genera known to occur in the Australasian region are *Stilobezzia, Acanthohelea* and *Monohelea*.

(*In the remaining groups the median fork is sessile.*)

Macropeza Group.

The shape of the thorax as seen in dorsal view distinguishes this group from all the others. The thorax is distinctly narrowed anteriorly, even sharply pointed, and hence appearing rather conical and in some species even projecting well over the dorsal surface of the head. The group is not known to be represented in the Australasian region.

Palpomyia Group.

The major distinguishing features of this group are the normally anteriorly rounded thorax and the presence of R_{2+3} and hence two distinct radial cells, the second being considerably longer than the first, with R_{4+5} terminating well beyond the middle of the wing (Text-figure 10). Macrotrichia are absent. There may be a small spine or tubercle at the middle of the anterior margin of the scutum, and the legs are modified in various ways in different genera. In our region a number of genera of this group have been recognized, namely, *Palpomyia, Clinohelea, Heteromyia, Xenohelea, Johannsenomyia* and *Dicrohelea*.

Bezzia Group.

In this group R_{2+3} is absent (Text-figure 11) and hence there is only a single long radial cell. This together with the sessile median fork should serve to distinguish the group. So far two genera have been recognized from the Australasian region, namely, *Bezzia* and *Nilobezzia*, but for further details see Part III of this series.

KEY TO GENERA* OF CERATOPOGONIDAE KNOWN TO OCCUR IN THE AUSTRALASIAN REGION.

1. Cross-vein r-m absent (Text-figure 4). Eyes very widely separated. Female antennae with 12-14 segments only (14 in both Australasian genera) (*Leptoconops* Group) .. 2
   Cross-vein r-m present (Text-figures 5-11). Eyes not widely separated (Text-figure 12). Female antennae with 15 segments 3
2. Lamellae of female ovipositor elongate and tapering, equal in length to apical three segments of abdomen ....'........................ *Leptoconops*
   Lamellae of female ovipositor very short, not tapering, their length comparable to that of the terminal abdominal segment .... *Styloconops*
3. Empodium present and obvious in claws of female and usually in those of male (Text-figure 18) 4
   Empodium lacking or inconspicuous and hair-like in claws of both sexes (Text-figure 19)   9
4. Microtrichia conspicuous, macrotrichia sub-erect, not scale-like and often not covering greater part of wing surface, R_{4+5} always reaching well beyond middle of anterior margin of wing, radial cells distinct, the second longer than the first (Text-figure 6) ....
   .... *Atrichopogon*
   Microtrichia minute, macrotrichia abundant, covering greater part of wing surface, recumbent and scale-like, R_{4+5} often terminating about middle of anterior margin of wing, radial cells not usually distinct (Text-figures 5 and 7) .. (*Forcipomyia* Group) .. 5
5. Second radial cell longer than the first and very narrow, R_{4+5} terminating beyond middle of anterior margin of wing (Text-figure 7) .... *Lasiohelea*
   Second radial cell not obviously longer than the first (if not obliterated), R_{4+5} terminating about the middle of the anterior margin of wing ....'.. 6
6. Antennae of female with last 6 segments elongate. Empodium large and broad, modified for clinging .... *Pterobosca*
   Antennae of female with only 5 segments elongate. Empodium not excessively developed   7

7. Antennae of female with basal flagellar segments (4-10) transverse, short and broad, often
   with the first few broader than long (Text-figure 16) 8
   Antennae of female with basal flagellar segments (4-10) relatively longer, not transverse
   but round, vasiform or flask-shaped (Text-figure 15) .... *Forcipomyia*
8. Male without empodium .... *Apelma*
   Male with empodium developed as in female .... *Thyridomyia**
9. R_{4+5} terminating at middle of anterior margin of wing, first radial cell usually obliterated,
   second radial cell short and square-ended, macrotrichia usually reasonably abundant
   (Text-figure 8). Antennal segments sculptured (Text-figure 17) .... *Dasyhelea*
   R_{4+5} terminating beyond, and usually well beyond, middle of anterior margin of wing, radial
   cells otherwise conformed, macrotrichia abundant, sparse or absent. Antennal segments
   not sculptured 10
10. M_2 with its origin distal to r-m (median fork petiolate, e.g., Text-figures 3 and 9) 11
    M_2 with its origin proximal to, or immediately beneath r-m (median fork sessile) (Text-
    figures 10 and 11) 14
11. Wings short in relation to width (usually about 2·2, sometimes up to 2·5 times as long as
    wide), radial cells usually small and subequal, usually partially obscured by a dark
    spot, rest of wing often conspicuously spotted, microtrichia obvious, macrotrichia dense
    to very sparse (Text-figure 9). Humeral pits obvious (Text-figure 23). Claws of
    female equal and small on all legs (Text-figure 19) .... *Culicoides*
    Wings longer in relation to width (usually about 3 times as long as wide, in small species
    down to 2·5 times), radial cells well developed with the second usually considerably
    longer than the first, microtrichia not always obvious, macrotrichia restricted to distal
    portion of wing or absent, wings seldom spotted (Text-figure 3). Humeral pits usually
    inconspicuous. Claws of female not equal and small on all legs (*Stilobezzia* Group) 12
12. All femora armed with spines .... *Acanthohelea*
    All femora without spines 13
13. Femora of hind legs thickened. Claws of female unequal on hind legs only .. *Monohelea*
    Femora of hind legs not thickened. Claws of female unequal on all legs (Text-fig. 20)
    .... *Stilobezzia*
14. R_{2+3} present, hence two distinct radial cells 15
    R_{2+3} absent, only one radial cell (Text-figure 11) 20
15. Fifth segments of tarsi not armed with strong spines 16
    Fifth segments of tarsi armed with strong spines (Text-figure 22) 18
16. Fifth tarsal segments of forelegs inflated; fourth tarsal segments of four posterior legs
    bilobed and armed with spines, femora unarmed .... *Clinohelea*
    Fifth tarsal segments of forelegs not inflated; fourth tarsal segments not armed, femora
    armed 17
17. Femora of forelegs greatly swollen with fore tibiae strongly curved to the outline of the
    femora (Text-figure 21) .... *Heteromyia*
    Femora of forelegs normal or if swollen then not to such an extent that the tibiae are curved
    to fit the outline of the femora .... *Palpomyia*
18. Claws of female equal and barbed on forelegs, unequal and barbed on four posterior legs
    .... *Dicrohelea*
    Claws of female otherwise 19
19. Claws of female unequal and simple on all legs (Text-figure 22) .... *Xenohelea*
    Claws of female all equal and barbed .... *Johannsenomyia*
20. Femora of at least the forelegs armed with stout spines; fifth tarsal segments not armed
    .... *Bezzia*
    Femora without stout spines, at most spinules (strengthened hairs) present on four posterior
    legs; fifth tarsal segments armed with strong spines .... *Nilobezzia*

Genus CERATOPOGON Meigen.
(Including *Brachypogon* Kieffer.)

Despite the fact that Skuse (1889) placed all of his species except one in the genus
Ceratopogon and Kieffer (1917) allocated ten species to this genus, including five of
Skuse's species and one of Schiner's, and a further one of Skuse's species to the genus
Brachypogon, there is still no evidence that the genus, as it is now understood, occurs
in Australia.† Most of the species retained in *Ceratopogon* by Kieffer really belong

---

* The genus *Thyridomyia* does not necessarily occur in the Australasian region but is
included here in case of possible confusion with *Apelma*, when only female specimens may be
available. For practical purposes it would perhaps be best to regard *Apelma* and *Thyridomyia*
as merely subgenera of *Forcipomyia*.

† Edwards (1926) described *Ceratopogon* (*Isohelea*) *peregrinator* from Savaii (Samoa), so
it seems possible that *Ceratopogon* may eventually be found westward of Samoa, at least in the
tropical part of the region.

Z

to the genus *Forcipomyia*, due to Kieffer's misconception of the genotype of *Ceratopogon* (see Edwards, 1926, page 407), and a few are obviously species of *Atrichopogon*. Only one species has really remained in doubt, and that is Skuse's *Ceratopogon imperfectus*, usually called by Kieffer *Brachypogon imperfectus*. My preliminary examination of the type specimen, mounted in gum on a card, left me in doubt as to which genus this species really belonged, since little beyond the wing venation could be made out in the specimen. However, on remounting in euparal it was immediately obvious that the specimen belonged to the Chironomidae and not the Ceratopogonidae at all, and should now be called *Spaniotoma (Smittia) imperfectus*.

It should be noted that in the one publication Kieffer (1906) placed this same species in both *Chironomus* (p. 19) and *Brachypogon* (p. 59), but in his 1917 revision he mentions it only in the genus *Brachypogon*.

References.

BUCKLEY, J. J. C., 1933.—A note on the Development of *Filaria ozzardi* in *Culicoides furens* Poey. *J. Helminth.*, 11 : 257-8.

————, 1934.—On the Development in *Culicoides furens* Poey, of *Filaria (Mansonella) ozzardi* Manson 1897. Ibid., 12 : 99-118.

————, 1938.—On *Culicoides* as a Vector of *Onchocerca gibsoni* (Cleland and Johnston, 1910). Ibid., 16 : 121-158.

CARTER, H. F., 1921.—A Revision of the Genus *Leptoconops*, Skuse. *Bull. ent. Res.*, 12 : 1-28.

————, INGRAM, A., and MACFIE, J. W. S.—1920.—Observations on the Ceratopogonine Midges of the Gold Coast with Descriptions of New Species. Parts 1-2. *Ann. Trop. Med. and Parasit.*, 14 : 187-270.

CLELAND, J. B., DODD, S., and FERGUSON, E. W., 1916.—Further Investigations into the Etiology of Worm Nests in Cattle. No. 2. Commonwealth of Aust. Publication (undated).

DICKINSON, C. G., and HILL, G. F., 1916.—Investigations into the cause of Worm Nodules in Cattle. Commonwealth of Aust. Publication.

EDWARDS, F. W., 1926.—On the British Biting Midges (Diptera, Ceratopogonidae). *Trans. ent. Soc. Lond.*, 1926 : 389-426.

————, 1928.—Ceratopogonidae. Insects of Samoa, Part 6, fasc. 2. Nematocera. Brit. Mus. (Nat. Hist.), 47-58.

ENDERLEIN, G., 1936.—Zweiflüger : Diptera. *Tierwelt Mitteleur.*, 6 : 49-53 (not seen).

GOETGHEBUER, M., 1920.—Ceratopogoninae de Belgique. *Mem. Mus. Nat. Hist. Belg.*, 8, fasc. 3 : 1-116.

INGRAM, A., and MACFIE, J. W. S., 1931a.—New Zealand Ceratopogonidae. *Ann. Trop. Med. and Parasit.*, 25 : 195-209.

————, ————, 1931b.—Ceratopogonidae. Diptera of Patagonia and South Chile, Part 2, fasc. 1. Brit. Mus. (Nat. Hist.).

JOHANNSEN, O. A., 1943.—A Generic Synopsis of the Ceratopogonidae (Heleidae) of the Americas, a Bibliography, and a list of the North American Species. *Ann. ent. Soc. Amer.*, 36 : 763-791.

KIEFFER, J. J., 1906.—Chironomidae. Wytsman's Genera Insectorum, fasc. 42 : 44-78.

————, 1917.—Chironomides d'Australie. *Ann. Mus. Nat. Hung.*, 15 : 177-199.

————, 1925.—Chironomidae Ceratopogoninae. Faune de France, 11 : 1-139.

————, 1926.—Ceratopogoninae : Clé de Détermination des Genera. *Arch. Inst. Past. Alger.*, 4 : 96-107.

MACFIE, J. W. S., 1932.—New Zealand Biting Midges (Diptera, Ceratopogonidae). *Ann. Trop. Med. and Parasit.*, 26 : 23-53.

————, 1939a.—The Diptera of the Territory of New Guinea, x, Family Ceratopogonidae. PROC. LINN. Soc. N.S.W., 64 : 367-8.

————, 1939b.—A Note on the Re-examination of Australian Species of Ceratopogonidae (Diptera). Ibid., 64 : 555-558.

————, 1940.—The Genera of Ceratopogonidae. *Ann. Trop. Med. and Parasit.*, 34 : 13-30.

MACKERRAS, I. M., and MACKERRAS, M. J., 1940.—Experimental Studies of Ephemeral Fever in Australian Cattle. Commonwealth of Aust. Counc. Sci. Ind. Res. Bull. 136 : 1-116.

MALLOCH, J. R., 1917.—A Preliminary Classification of Diptera, Exclusive of Pupipara, Based upon Larval and Pupal Characters, with Keys to Imagines in certain Families. Part 1. *Bull. Ill. State Lab. Nat. Hist.*, 12 : 281.

MANSON, P., 1892.—The Geographic Distribution, Pathological Relations and Life History of *F. sanguinis hominis diurna* and of *F. sanguinis hominis perstans* in Connection with Preventive Medicine. Trans. 7th Inter. Cong. of Hyg. and Demography. London, 1 : 79.

DE MEIJERE, J. C. H., 1915.—Diptera in Nova Guinea, 5, Zoologie : 69.

————, 1917.—Diptera aus Nord-Neu-Guinea. *Tijdschr. v. Ent.*, 58 : 98.

DE MEILLON, B., 1936.—South African Ceratopogonidae. Part 2. Some New and Unrecorded Species. Publications of South African Institute for Medical Research, No. 38. Vol. 7. Studies of Insects of Medical Importance in South Africa, Part 3, No. 5: 141-207.

PAINTER, R. H., 1926.—The Biology, Immature Stages, and Control of the Sandflies (biting Ceratopogonidae) at Puerto Castilla, Honduras. United Fruit Co., Med. Dept. Ann. Rept., 245-262 (not seen—quoted in Thomsen, 1937).

SCHINER, J. R., 1868.—Diptera der Novara Expedition. Zool. Theil. Bd., 2 : 26 (not seen, quoted in Skuse, 1889).

SEDDON, H. R., 1938.—The Spread of Ephemeral Fever (Three Day Sickness) in Australia in 1936-37. Q'ld. Agric. J., 50 : 601-9.

SHARP, N. A. E., 1928.—Filaria perstans : Its Development in Culicoides austeni. Trans. Roy. Soc. Trop. Med. and Hyg., 21 : 371-396.

SKUSE, F. A. A., 1889.—Diptera of Australia. Part 6—The Chironomidae. PROC. LINN. SOC. N.S.W., 4 (2nd series) : 286-311.

STEWARD, J. S., 1933.—Onchocerca cervicalis (Railliet and Henry, 1910) and its Development in Culicoides nubeculosus Mg. Univ. of Cambridge, Inst. of Animal Pathology. Rept. of the Director, 3 (1932-33) : 272-284.

TAYLOR, F. H., 1911.—Report of the Entomologist. Rept. Aust. Inst. Trop. Med., 1911 : 73.

————, 1918.—Phlebotomic Diptera. Aust. Zoologist, 1 : 169.

THOMSEN, L. C., 1937.—Aquatic Diptera, Part 5. Ceratopogonidae. Cornell. Univ. Agric. Expt. Sta. Mem., 210 : 57-80.

AUSTRALASIAN CERATOPOGONIDAE (DIPTERA, NEMATOCERA).

PART II. THE LEPTOCONOPS GROUP OF GENERA.

By David J. Lee, B.Sc.

(Plate xxi, 13 Text-figures.)

[Read 29th October, 1947.]

In this part Australasian species of the genera *Leptoconops* (four species) and *Styloconops* (three species) are discussed, one species being described as new in each of the two genera.

LEPTOCONOPS GROUP.

Two genera from this group are known to occur in the Australasian region, namely *Leptoconops* and *Styloconops*. Records of the species are few, but they must be fairly widely distributed. Probably all bite man, but only the species from New Guinea and New Zealand appear to occur in large numbers and hence cause considerable annoyance. Information on the life histories of these insects, about which nothing is known in this region, should prove particularly interesting.

Genus LEPTOCONOPS Skuse (sens. lat.).

Skuse, F. A., 1889.—Proc. Linn. Soc. N.S.W., 4 (2nd series) : 288.
Carter, H. F., 1921.—*Bull. ent. Res.*, 12 : 5.

Synonymy: Macfie (1940) places the following in the synonymy of *Leptoconops*: *Tersesthes* Towns. 1893; *Centrotypus* Grassi 1901; *Mycterotypus* Lutz 1912, nec Phil; *Schizoconops* K. 1918; *Protersesthes* K. 1921.

Holoconops K. 1918 and *Microconops* K. 1921 are treated as separate genera but it seems desirable, for practical purposes, to follow Carter's (1921) system of classification in regarding these as merely subgenera.

Genotype: *Leptoconops stygius* Skuse loc. cit. (By monotypy.)

Subgenus LEPTOCONOPS (Skuse) Carter.

Carter, H. F., 1921.—*Bull. ent. Res.*, 12 : 10.

SUBGENERIC CHARACTERS.

(With the exception of the number of antennal segments these apply equally well to the other subgenera of *Leptoconops*, which are not, however, recorded from the Australasian region.) The eyes are widely separated, with the frons bare or with only one pair of bristles between the eyes. The mouthparts are less than or equal in length to the height of the head. The palpi are only four-segmented, with the first and second segments reduced, the third large and swollen and the fourth of approximately the same length as the third, but not swollen. The male palpi are somewhat longer and the third segment is not swollen. The female antennae comprise fourteen segments, the first being little more than a chitinous ring, the second (the pedicel) large and rounded, and the third rather intermediate in size between the second and the fourth and succeeding flagellar segments. Segments 4 to 13 are small, transverse or subspherical, and the terminal segment is considerably longer than the preceding one. The male antennae comprise fifteen segments with normal plumes on the flagellum and the terminal segment considerably lengthened.

The venation of the wings is rather indistinct. The costa does not extend to the middle of the wing and the branches of the radius are largely fused distally with the costa. Carter (1921, p. 8) and de Meillon (1936, p. 142) both consider the first

apparent vein extending from near the base of the wing to the apex as a spurious one; this does seem the only interpretation which will not be a direct negation of the interpretation adopted for all other Ceratopogonidae. The radio-median cross-vein is absent and M_2 may be interrupted at the base. Microtrichia are present over the wing surface but macrotrichia are absent.

The legs are moderately long, the posterior pair being the longest. The femora are unmodified and unarmed. There is a short, sharp ventral spur at the tip of each tibia, the first tarsal segment of the fore- and mid-legs is about twice the length of the second and in the hind legs about 1·5 times its length. The second to fourth tarsal segments are cylindrical, decreasing in length, but the fifth is usually distinctly longer than the fourth. Some of the bristles of the first tarsal segments may be developed as spines, particularly the apical ones.

The female abdomen is terminated by two exceedingly long, narrow, tapering lamellae. In the male the hypopygium is large and conspicuous.

Key to Australasian Species of the Leptoconops Group.

1. Lamellae elongate, considerably longer than wide (Genus *Leptoconops*) 2
   Lamellae not longer than wide (Genus *Styloconops*) 5
2. Larger species. Wing length 2·0 mm. or more; length of antenna 0·62 mm. or more 3
   Smaller species. Wing length 1·6 mm. or less; length of antenna 0·52 mm. or less 4
3. Antenna very long, last segment at least six times as long as broad .. *L. longicornis* Cart.
   Antenna shorter, last segment at most 3·5 times as long as broad .... *L. grandis* Cart.
4. Larger species; segment 3 of palpus 1·7 times segment 4; wing length 1·3-1·6 mm. ....
   .... *L. stygius* Sk.
   Smaller species; segment 3 of palpus 1·3 times segment 4; wing length 1·1-1·2 mm. ....
   .... *L. woodhilli* n. sp.
5. Frons covered with numerous strong, short spines .... *S. australiensis* n. sp.
   Frons with sparse hairs only 6
6. First hind tarsus two-thirds length of tibia; distal half of femora not contrasting in colour
   with basal half .... *S. myersi* (Tonn.)
   First hind tarsus one-half length of tibia; distal half of femora dark brown in strong
   contrast to lighter brown of basal half .... *S. albiventris* (de Meij.)

LEPTOCONOPS (LEPTOCONOPS) STYGIUS Skuse.

SKUSE, F. A., 1889.—PROC. LINN. Soc. N.S.W., 4 (2nd series): 288.
CARTER, H. F., 1921.—*Bull. ent. Res.*, 12: 10-11.

Type: Type ♀ in Macleay Museum, University of Sydney.

Type Locality: Woronora (near Sydney, New South Wales).

DISTINCTIVE CHARACTERS.

(See Plate xxi, fig. 3, for photograph of wing and Text-figs. 1-3 for drawings of head, palpus and terminal abdominal segments.)

L. stygius is an entirely dark species with hyaline wings. The eyes are widely separated, with only a pair of frontal bristles at the level of the top of the eyes. The antennae are short with the flagellar segments spherical, except 14, which is about 1·6 times as long as broad. The scutum is clothed with minute black hairs, the legs are without any obvious modifications and the claws are equal and simple (but with a bristle arising from the base of each). The lamellae of the abdomen are elongate, bluntly rounded distally and 0·22 the length of the wing. There are two spermathecae, both heavily chitinized, subspherical (30μ) with the commencement of the duct chitinized for a short distance.

The shape of the antennae, and in particular that of the terminal segment, will distinguish this species from *L. longicornis* and *L. grandis*, but only the measurements of various parts, such as the palpi, the antennal segments and the wings, will distinguish it from *L. woodhilli*.

The male and the larva are both unknown.

Distribution: The type locality and Fitzroy Falls (A. Tonnoir, 22-27.xi.1937). Additional material in C.S.I.R. Museum.

LEPTOCONOPS (LEPTOCONOPS) WOODHILLI, n. sp.

Types: Holotype ♀ (mounted on slide) and four paratype ♀♀ in the C.S.I.R. Museum. Three paratype ♀♀ (one mounted on slide) in the Macleay Museum, University of Sydney.

Type Locality: Adelaide River, Northern Territory (A. R. Woodhill, 1: 1943).

I have compared a series of seven specimens of *Leptoconops* from Adelaide River with a series of fourteen specimens of *L. stygius* from Fitzroy Falls and although there are no really obvious differences between the two, the measurements of various parts are so consistently at variance that I feel the Northern Territory representative of this genus should, for the present at least, be treated as distinct. The genus *Leptoconops* is very imperfectly known in Australia and the fact that no males or larvae of any species are as yet known makes it exceedingly difficult to arrive at a satisfactory interpretation of specific differences.

DISTINCTIVE CHARACTERS.

(See Plate xxi, fig. 2, for photograph of wing.) *L. woodhilli* is again a uniformly black species somewhat smaller than *L. stygius* (the difference in size is quite obvious to the naked eye in pinned specimens when the two species are compared). Structurally there are no differences between the two, but the measurements of almost all parts of *L. woodhilli* are smaller than those of *L. stygius* and in particular those of the wings, the antennae, the palpi and the hind legs. The relative lengths of the third and fourth segments of the palpi also do not correspond. A comparative table (Table 1) gives the details of the meaurements of *L. woodhilli* in relation to other species.

Distribution: As yet this species is only known from the type locality.

LEPTOCONOPS (LEPTOCONOPS) LONGICORNIS Carter.

CARTER, H. F., 1921.—*Bull. ent. Res.*, 12: 11-12.

Types: Two cotype ♀♀ in the British Museum (Natural History).

Type Locality: Stated as the interior of Western Australia. The collector of these specimens, Professor W. J. Dakin, informs me that they were certainly not taken at any great distance from the coast and probably in the vicinity of Perth.

DISTINCTIVE CHARACTERS.

(See Plate xxi, fig. 4, for photograph of wing, and Text-figs. 4–6 for head, palpus and terminal segments of abdomen.)

This is a rather larger species than *L. stygius* and is particularly distinct on antennal characters. The length of the antennae is 0·84 mm. or almost twice that of *L. stygius*, the flagellar segments being subspherical to narrowly oval (1·0 to 2·1 times as long as broad) and the terminal segment is 6·5 times as long as broad, whereas in *L. stygius* it is less than twice as long as broad.

Neither the male nor the larva is known.

Distribution: I have examined a large series from Crawley, W.A. (D. Swan, 1.vii.1931), and a further series from Katanning, W.A. (M. M. H. Wallace, 9.v.1947, biting man freely at 3.30 p.m.). Additional material in the C.S.I.R. Museum.

LEPTOCONOPS (LEPTOCONOPS) GRANDIS Carter.

CARTER, H. F., 1921.—*Bull. ent. Res.*, 12: 12-13.

Types: Two ♀♀ cotypes in British Museum (Natural History).

Type Locality: Stated as interior of Western Australia but see remarks under *L. longicornis*.

DISTINCTIVE CHARACTERS.

According to Carter this species is almost identical with *L. longicornis* except in the form of the antenna. The length of this organ is 0·62 mm. (0·84 in *L. longicornis*), the individual segments of the flagellum (4–13) are subspherical, being from 1·0 to 1·1 times as long as broad and the terminal segment is almost 3·5 times as long as broad (6·5 in *L. longicornis*) and as long as the preceding 2½ segments (preceding 3 in *L. longicornis*).

The male and the larva are again unknown.

Distribution: I have not seen this species and there are no further records of its distribution in Western Australia.

Genus STYLOCONOPS Kieffer.

KIEFFER, J. J., 1921.—*Arch. Inst. Past. de l'Afr. du Nord.*, 1 : 107.
    Synonymy: *Acanthoconops* Carter, H. F., 1921. *Bull. ent. Res.*, 12 : 24.
    Genotype: *Styloconops albiventris* (de Meijere). (By original designation.)

GENERIC CHARACTERS.

The genus *Styloconops* only differs from *Leptoconops* in having the area between the eyes (the frons) clothed with short spines and the lamellae very short, actually broader than long. As in *Leptoconops* (sens. str.) there are fourteen segments in the female antenna. The sensory area on the third segment of the palpus is a single large pit, whereas in at least the Australasian species of *Leptoconops* the sensory area consists of a group of numerous small pits.

STYLOCONOPS ALBIVENTRIS (de Meijere).

DE MEIJERE, J. C. H., 1915.—*Tijdschr. v. Ent.*, 58 : 98 (*Leptoconops*).
    Types: Location of types not stated.
    Type Locality: Mouth of Sernowai River, New Guinea.
    Synonymy: *Leptoconops spinosipes* Kieffer, J. J., 1917. *Ann. Mus. Nat. Hung.*, 15 : 190.
(Type locality: Tamara, Berlinhafen, New Guinea.) *Acanthoconops albiventris* Carter, H. F., 1921. *Bull. ent. Res.*, 12 : 26.

DISTINCTIVE CHARACTERS.

(See Plate xxi, fig. 1, for photograph of wing, and Text-figs. 7–10 for head, palpus, fore tarsus and terminal segments of abdomen.)

An entirely dark species except for the abdomen, which is often white laterally in expanded unfed specimens. It may readily be distinguished from the species of *Leptoconops* by the small fine spines on the frons and the prominent spines on the legs. Reference to Table 1 and Text-figures 7–10 will further clarify its specific characters. Differentiation from *S. myersi* and *S. australiensis* is clarified under those species.

This is undoubtedly an extremely prevalent and annoying insect on the New Guinea coast.

Distribution: Apart from the type locality records Macfie (1939) has identified specimens of this species from Aitape (New Guinea) and Rabaul (New Britain) and from the Marquesas (1933). I have examined a large series of female specimens also from Aitape and Finschhafen (both M. H. Wallace), Busama, 12.v.1947 (A. J. Bearup), and Gona, 12.xi.44 (H. A. Grandall). Additional material in both Macleay Museum, Sydney University, and C.S.I.R. Museum, Canberra, A.C.T.

STYLOCONOPS MYERSI (Tonnoir).

TONNOIR, A. L., 1923.—*Bull. ent. Res.*, 14 : 443 (*Acanthoconops*).
    Type: Holotype ♀ in Cawthron Institute, Nelson, New Zealand. Several paratypes in School of Public Health and Tropical Medicine, Sydney, one paratype in C.S.I.R. Museum, Canberra, A.C.T.
    Type Locality: Taputaputa, Spirit Bay, North Island, New Zealand.
    Synonymy: *Acanthoconops myersi*, Tonnoir, loc. cit.

DISTINCTIVE CHARACTERS.

This species is very similar to *S. albiventris* and according to Tonnoir "the only differences are in the scanty hair on the frons, the untoothed tarsal claws, and the length of the hind metatarsi, which is two-thirds that of the tibia instead of one-half".

I have compared a paratype of *S. myersi* with specimens of *S. albiventris* and found that there is no difference in the frons nor in the claws but that the difference in relative length of the hind tibiae and first tarsi does hold. In *S. myersi* the hind tibia is 1·6 × the length of the first tarsal segment and 2·1 × in *S. albiventris*. In addition the femora of *S. myersi* are almost uniformly brown whereas the apical half is considerably darker than the basal half in *S. albiventris*.

There is no doubt the two species are very closely similar and both are serious pests of man where they occur abundantly.
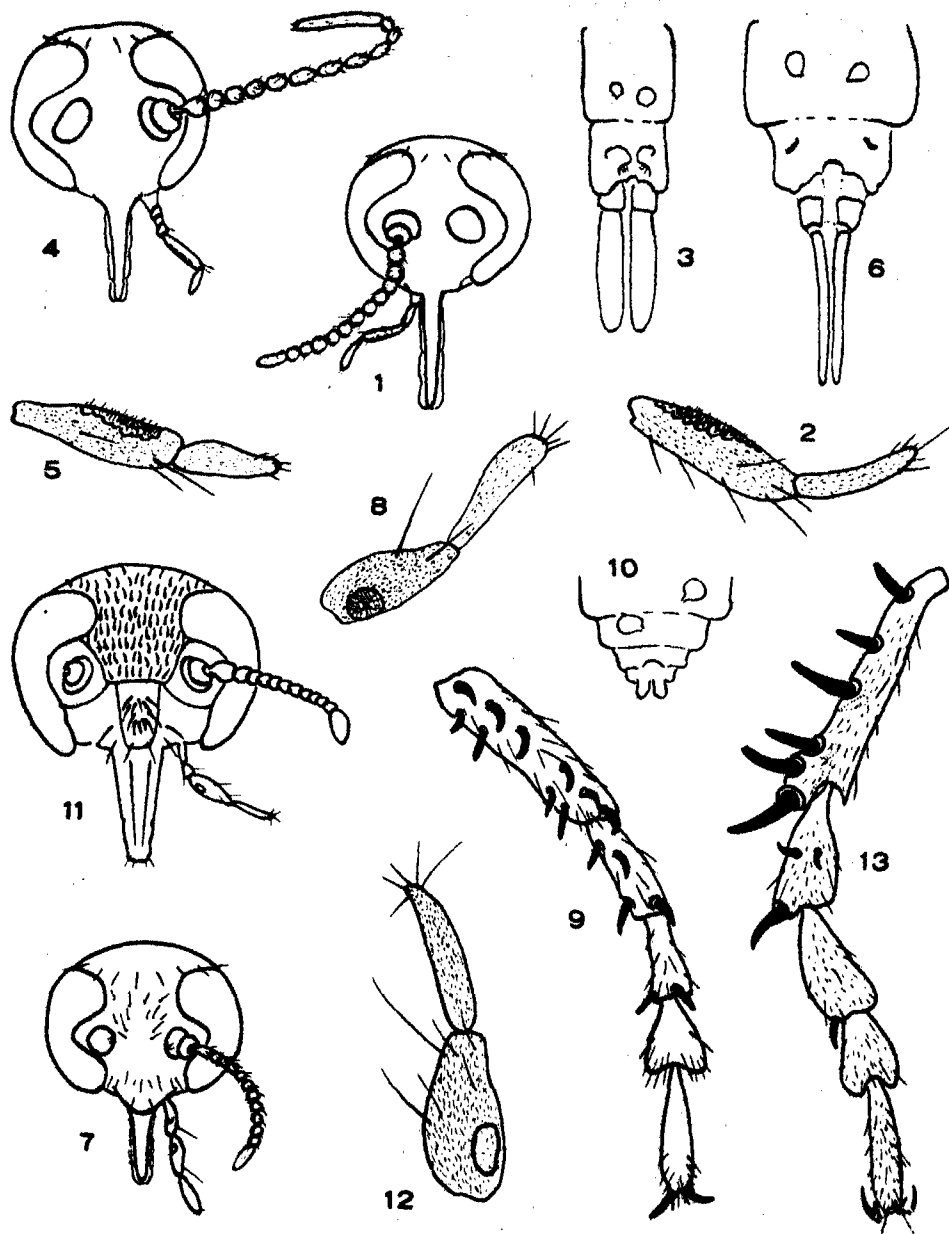
Text-figures 1-13.—Various species of the *Leptoconops* group.

Figs. 1-3.—*Leptoconops stygius.* 1, Anterior view of head. 2, Segments 3 and 4 of palpus. 3, Terminal segments of abdomen.

Figs. 4-6.—*Leptoconops longicornis.* 4, Anterior view of head. 5, Segments 3 and 4 of palpus. 6, Terminal segments of abdomen.

Figs. 7-10.—*Styloconops albiventris.* 7, Anterior view of head. 8, Segments 3 and 4 of palpus. 9, Tarsus of foreleg. 10, Terminal segments of abdomen.

Figs. 11-13.—*Styloconops australiensis.* 11, Anterior view of head. 12, Segments 3 and 4 of palpus. 13, Tarsus of foreleg.

(Magnifications: Figs. 1, 4, 7 and 11 × 64; Figs. 2, 5, 8 and 12 × 236; Figs. 9 and 13, × 250; Figs. 3, 6 and 10, × 66.)

TABLE 1.

Measurements of Leptoconops *Group.*

	L. stygius.	L. woodhilli.	L. longicornis.	L. grandis.	S. australiensis.	S. albiventris.	S. myersi.
	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Body	2·5		(3·5)	(3·5)	2·1	1·6 (1·8)	1·5
Wing	1·47	1·14	(2·2)	(2·0)	1·6	1·05–1·19	1·15
	(Average of 14 specimens)	(Average of 7 specimens)					
Palpus	0·286	0·182				0·150	
Third segment of palpus	0·110	0·065				0·075	
Fourth segment of palpus	0·065	0·050				0·080	
Antenna (total)	(0·48)*–0·52	0·416	(0·84)	(0·62)	0·36	0·380	
Segment 2	0·050 long × 0·065 wide	0·040×0·050				0·045×0·055	
,, 3		0·035×0·035					
,, 4		0·020×0·030					
,, 5		0·025×0·030				0·025×0·033	
,, 6	0·035×0·035	0·025×0·030				0·025×0·033	
,, 12	0·035×0·035	0·030×0·020				0·025×0·028	
,, 13	0·035×0·035	0·030×0·018				0·065×0·030	
,, 14	0·075×0·040	0·070×0·020			0·065	0·070	0·060
Fore leg—							
Femur	0·425	0·340			0·391	0·300	0·300
Tibia	0·425	0·306			0·391	0·300	0·325
Tarsus I	0·170	0·136			0·153	0·120	0·135
,, II	0·085	0·068			0·068	0·060	0·065
,, III	0·068	0·068			0·068	0·050	0·060
,, IV	0·034	0·026			0·051	0·045	0·040
,, V	0·060	0·068			0·068	0·060	0·070
Hind leg—							
Femur	0·646	0·391			0·64	0·450	0·450
Tibia	0·476	0·340			0·64	0·375	0·450
Tarsus I	0·255	0·187			0·25	0·180	0·435
,, II	0·153	0·119			0·15	0·135	0·260
,, III	0·085	0·068			0·09	0·075	0·150
,, IV	0·026	0·034			0·065	0·045	0·100
,, V	0·068	0·065			0·085	0·065	0·050

* Figures in brackets are quoted from other authors.

STYLOCONOPS AUSTRALIENSIS, n. sp.

Types: Holotype ♀ and 2 ♀♀ paratypes in the C.S.I.R. Museum. All specimens mounted on slides.

Type Locality: Pittwater, New South Wales, 14.xii.1946 (D. J. Lee). The specimens were taken biting man.

DISTINCTIVE CHARACTERS.

This is a very dark species except for the almost white abdomen, pale bases to femora, lighter brown tarsi and conspicuously white halteres. The excessively spiny frons immediately distinguishes it from any other Australasian species in the *Leptoconops* group.

DESCRIPTION (Female).

Head: (Text-fig. 11.) The most remarkable feature of the almost black head is the excessively spiny frons similar to that of *S. spinosifrons* (Cart.) from Zanzibar, but apparently even more pronounced. The eyes are very widely separated and the

antennae 14-segmented, segments 4–13 being very short, actually broader than long, with segment 14 expanded and almost four times as long as the preceding segment. The palpi are 4-segmented, of which the first two are small, the second and third considerably longer and subequal, but 3 is also proximally distended with a rounded sensory pit (see Text-fig. 12.)

Thorax: This is very dark brown with creamy-white halteres.

Legs: (See Table I for measurements.) The bases of the femora are lighter brown than the rest of the femora and tibiae; the tarsi are lighter brown. On the forelegs both the first and second tarsal segments carry stout spines (Text-fig. 13). On the mid-legs tarsus I is invested with longer pointed spines and on the hind legs both tarsus I and II are strongly spinose. The claws are equal, each with a prominent tarsal tooth.

Wings: The wing length is 1·6 mm. They are very pale and similar to those of *S. albiventris*.

Abdomen: This is white in living specimens and with the tergites scarcely chitinized. The lamellae of the ovipositor are very short and the spermathecae two in number, rounded, with obvious chitinized ducts.

Distribution: Only known from the type locality.

References: Systematic references are cited in full in the text. Any other general references will be found cited in full in Part I of this series.

EXPLANATION OF PLATE XXI.

Figs. 1-4.—Photographs of wings of various species of the *Leptoconops* group. All × 50.

These photographs are the work of Mr. E. Parrish of the McMaster Laboratory, C.S.I.R. Division of Animal Health, University of Sydney. At the time of writing Mr. Parrish is not available to give details of the photographic methods used, but I hope to include these in a later part. The preparations from which the photographs were made were detached wings mounted in euparal except in the case of *S. albiventris*, for which species it was found necessary to mount in a non-clearing celluloid medium in order to get a satisfactory photograph. No staining was used for the purposes of these photographs.

Fig. 1.—*S. albiventris*, specimen from Aitape.

Fig. 2.—*L. woodhilli*, paratype.

Fig. 3.—*L. stygius*, specimen from Fitzroy Falls.

Fig. 4.—*L. longicornis*, specimen from Crawley, Western Australia.

AUSTRALASIAN CERATOPOGONIDAE (DIPTERA, NEMATOCERA).

PART III. THE BEZZIA GROUP OF GENERA.

By DAVID J. LEE, B.Sc.

(With Plate xxi, Fig. 5, and eight Text-figures.)

[Read 29th October, 1947.]

INTRODUCTION.

The present paper discusses four species included in the genus *Bezzia*, of which one is described as new, and one species, also new in *Nilobezzia*. The latter is the first record of this genus from the Australasian region. For the characters differentiating this group see Part I of this series.

Translations of Kieffer's original descriptions are included in order to facilitate re-recognition of his species. In these translations Kieffer's interpretations of the number of segments in the antennae and palpi and his terminology of wing venation, are adjusted to present conceptions. Although his type specimens were from the National Museum of Hungary, Budapest, I have been unable to find out whether or not they are still in existence.

Genus BEZZIA Kieffer.

KIEFFER, J. J., 1899.—*Bull. Soc. ent. France*, 68 : 69.
Genotype (by original designation) : *B. ornata* (Meigen).

GENERIC CHARACTERS.

This genus does not seem to have been adequately defined, but the following combination of the characters given by Goetghebuer (1920) and Edwards (1926) should provide a workable definition. The genus has many of the characteristics of *Palpomyia* but an anterior tubercle is lacking, as also is R_{2+3} (hence only a single radial cell); R_{4+5} terminates between the middle and the extremity of the wing and the median fork is sessile. Macrotrichia are restricted or absent. Femoral spines may be present or absent and the fourth tarsal segment is short and cordate and without spines.

For the present I have included all species conforming generally with the above definition in the genus *Bezzia* with the exception of one species which I feel is without doubt a *Nilobezzia*. The species *B. curticornis* may later require to be placed in some other closely related genus and Skuse's *Ceratopogon latipennis*[*] is only doubtfully placed here, but owing to damage to the type its position must remain obscure until it is again collected and recognized.

Key to Known Australasian Species included in Bezzia.

1. R_{4+5} extending at least to distal fourth of wing 2
   R_{4+5} scarcely passing the middle of the wing, macrotrichia present on the distal half of the wing .... *latipennis* (Sk.)
2. All femora armed with black spinules; fifth tarsal segment with 5 pairs of cylindrical black spinules .... *curticornis* K
   Only anterior femora armed with spines 3
3. Anterior femora armed with 5-6 black spines; fifth tarsal segment bare of spines ....
   .... *australiensis* K
   Anterior femora with one spine only .... *tasmaniensis* n. sp.

---

[*] Kieffer (1906) placed this species in both *Didymophleps* (p. 56) and *Bezzia* (p. 58), although in 1917 he considered it as a *Didymophleps*. His earlier confusion does indicate that he regarded it as at least related to *Bezzia*.

BEZZIA LATIPENNIS (Skuse).

SKUSE, F. A., 1889.—PROC. LINN. SOC. N.S.W., 4 (2nd series): 308. (*Ceratopogon.*)
KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 193. (*Didymophleps.* *)

Type: All that remains of the unique female type is what is apparently a hind leg. In Macleay Museum, University of Sydney.

Type Locality: Berowra, New South Wales.

Synonymy: *Ceratopogon latipennis*, Skuse, loc. cit. *Didymophleps* * *latipennis*, Kieffer, J. J., 1906. Chironomidae in Wytsman's Genera Insectorum, fasc. 42: 56. *Bezzia latipennis*, Kieffer, loc. cit., 58.

Note: Until this species is rediscovered it will be impossible to place it with certainty in its correct genus. It does, however, seem likely that it will fall into the *Bezzia* group of genera because of the single radial cell.

DISTINCTIVE CHARACTERS.

It should prove a simple matter to recognize this species again. It is dull brownish in colour with yellow legs, of moderately large size (wing 1·89 mm. long) and there is only a single radial cell and the apical half and posterior border is clothed with a minute yellowish pubescence. The tarsal claws are very long (see Text-fig. 1).
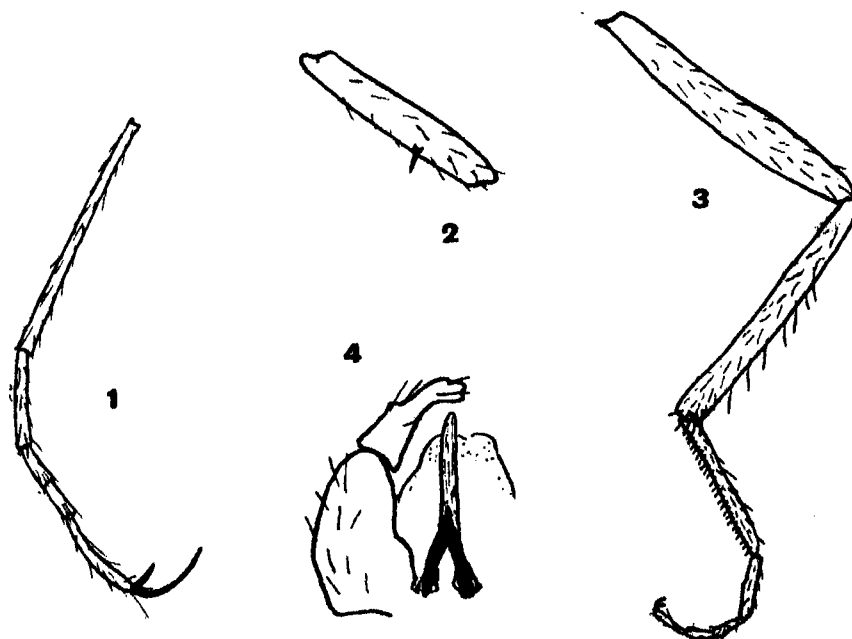
Text-figures 1-4.—1, Hind tarsus of *Bezzia latipennis*, × 100. 2, Fore femur of *B. tasmaniensis* (male), × 100. 3, Hind leg of *B. tasmaniensis* (male), × 100. 4, Male genitalia of *B. tasmaniensis*, × 336. All figures from holotype specimens.

BEZZIA CURTICORNIS Kieffer.

KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 196.

Type: Presumably in National Museum of Hungary, Budapest.

Type Locality: Botanic Gardens, Sydney, New South Wales.

Translation of Original Description.

"♀. Tawny yellow, dull and pruinose. Eyes separated by their terminal breadth, the third segment of the palpi a little enlarged, as long as the fourth and fifth together, the latter subequal. Antennae brown, short, not attaining the wing base, scape reddish-brown, segments 4-10 compact, briefly elliptical, scarcely as long as wide, segments 11-15 cylindrical, together as long as 3-10 together, each twice as long as wide. Thorax strongly convex, higher than long, without a spinule in front. Mesonotum glabrous, with a median band of a dull brown, linear,

* Kieffer, however, used the incorrect spelling *Didymorphleps* for this genus.

divided by a fine longitudinal line, shortened behind; the anterior third and the sides of the mesonotum equally brownish black. Scutellum pale yellow, with long hairs. Halteres pale yellow. Wings whitish, almost rectangular at the lobe, with an indistinct dark spot situated in the fork of the anal vein, R_{4+5} attaining the last fifth of the wing, not passed by the costa, closer to the wing point than M_{1}, at least twice as long as R_1, its base very oblique and longer than r-m, the latter perpendicular, bifurcation of M proximal to r-m, the M_{3+4}-Cu_1 fork situated under r-m, M_{3+4} continuing the direction of the stem, Cu_1 very oblique. Legs moderately large, pale yellow, fifth tarsal segment black, the distal half of all the femora armed with black spinules, these longer than ordinarily, attaining in length half the width of the femora, six or seven on the four anterior femora, four or five on the two posterior femora, the two posterior legs having also on the femora, the tibiae and the tarsi, hairs as long, the four anterior with shorter hairs; posterior tarsi distinctly longer than the tibiae, third segment of all the tarsi cylindrical, two to three times as long as wide, fourth scarcely as long as wide, obliquely truncated but not lobed, the fifth almost as long as the third and fourth together, slender, curved with five pairs of cylindrical black spinules; tarsal claws large, attaining two-thirds of the segment, equal, bifid, the two branches unequal, the larger almost three times as long as the smaller. Abdomen whitish-yellow, flattened, as large as the thorax. Length 3 mm."

Distribution: This species has not yet been rediscovered.

BEZZIA AUSTRALIENSIS Kieffer.

KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 197.
    Types: Presumably in National Museum of Hungary, Budapest.
    Type Locality: Botanic Gardens, Sydney, New South Wales.

Translation of Original Description.

"♀. Brownish-black, dull, head brown. Antennae separated by a triangular space narrowing to a fine line in front. Fifth segment of the palpi a little longer than the fourth, shorter than the third, without long hairs. Antennae attaining the posterior border of the thorax, segments 4-10 cylindrical, a little longer than wide, segments 11-15 together a little longer than 3-10 together, filiform, each a little more than twice as long as 10. Thorax strongly convex, higher than long, without spinule in front. Mesonotum glabrous, with three longitudinal bands of reddish-brown, the median linear, bordered by a clearer colour, the laterals shortened in front; shoulders with three or four little white spots. Scutellum with several hairs. Petiole of the halteres pale. Wings hyaline, gradually thinning to the base, R_{4+5} not passed by the costa, 2·5 times as long as R_1 (at least) attaining the last quarter of the wing, further distant from the wing point than M_1, but closer than M_{3+4}, in its distal half it approaches the costa and the narrow space which separates them is darkened; bifurcation of M proximal to r-m, the base of Cu_1 on M_{3+4} is distal to the r-m; intercalary fork absent, as usual in this genus. Legs slender, femora, tibiae of the two anterior legs with two yellow rings, intermediate tibiae with one yellow ring near their distal extremities, posterior tibiae with a large yellow ring near the middle and yellow at the base, tarsi all yellow, distal extremities of segments 1-3 and segments 4-5 black, anterior femora with five or six spines on its distal half, the others inermous, all the tarsi a little longer than the tibiae, third segment of the posterior tarsi at least twice as long as wide, fourth transverse, cordiform, fifth longer than the third, narrow, slender, inermous; claws of moderate length, one-third the length of the fifth segment with a minute tooth at their base. Abdomen flattened scarcely narrower than the thorax. Length 2-3 mm.

"Sydney, Botanic Gardens (Biró, 1900). Two females; a third specimen has the four posterior legs reddish, with the tibiae and tarsi yellow, the posterior tibia having near its extremity a black ring, and near its base, another larger one."

Distribution: This species has not been rediscovered.

Note: A specimen in the C.S.I.R. Museum from Blundell's, A.C.T. (7.i.1930, A. Tonnoir), would key to *B. australiensis*, but differs at least in its uniformly shiny dark brown scutum and darker legs. It is almost certainly a new species but is too damaged for description.

BEZZIA TASMANIENSIS n. sp.

    Type: Holotype ♂, in the C.S.I.R. Museum.
    Type Locality: Burnie, Tasmania (31.i.1923, A. Tonnoir).

DISTINCTIVE CHARACTERS.

A small species of uniformly dark-brown colouration (head, thorax and abdomen) with pale yellow-brown legs except for the tibiae, which are indefinitely slightly darker at the tip and anterior femora with only one spine.

DESCRIPTION (See Table I for measurements).

Male.

Head: The eyes are separated, the antennae short with segment 2 (the pedicel) very large, the two almost touching; segment 3 with a long stem but otherwise similar to the

following flagellar segments, 4 to 11 being equal in size, subcylindrical, a little longer than broad (6:4) and 12 to 15 are elongated, almost three times as long as wide, but 12 is slightly smaller than the other three and 15 slightly longer. There are sparse verticels of long hairs on segments 3–11.

Thorax: The scutum and scutellum are clothed with fine golden hairs, uniformly but sparsely distributed. The halteres are of the same colour as the thorax.

Legs: The femora of the forelegs (Text-fig. 2) have a single stout short spine on the under surface about two-thirds from the base and the tarsal claws are equal and simple on all legs. See Text-fig. 3 for illustration of hind leg.

Wings: The wings (Plate xxi, fig. 5) are covered with fine microtrichia but macrotrichia are absent. There is only one radial cell, R_{2+3} being absent, and R_{4+5} (and the costa) extend about five-sixths the length of the wing and M_2 arises underneath r-m.

Abdomen: The genitalia are of the usual Bezzia type, very small with the harpes fused into a long median rod. (See Text-fig. 4.)

The female is not known.

Distribution: Only known from the type locality.

TABLE 1.

Measurements of Species of the Bezzia Group.

| | | *Bezzia tasmaniensis* ♂ | | *Nilobezzia whartoni.* | |
				♀	♂
Wing—		mm.		mm.	mm.
Length	.. ..	1·105		2·430–2·538	1·350
Width	.. ..	0·391			
Antenna—					
Total length, segments 3–15	..	0·510			
Segments 4–10	..	Each 0·035			
Segment 12	..	0·045			
„ 13	..	0·050			
„ 14	..	0·050			
„ 15	..	0·060			
Legs—		Fore Leg.	Hind Leg.	Fore Leg.	Hind Leg.	Hind Leg.
Femur	.. ..	0·289	0·408	0·780	1·002	0·690
Tibia	.. ..	0·272	0·357	0·780	0·988	0·572
Tarsus I	..	0·111	0·187	0·384	1·040	0·390
„ II	..	0·051	0·085	0·169	0·234	0·143
„ III	..	0·034	0·034	0·104	0·169	0·104
„ IV	..	0·034	0·034	0·078	0·104	0·078
„ V	..	0·051	0·051	0·195	0·208	0·117
Claw	.. ..			0·169	0·195	0·039

Genus NILOBEZZIA Kieffer.

KIEFFER, J. J., 1921.—*Ann. Soc. Ent. France*, 90: 24.

MACFIE, J. W. S., 1934.—*Tijdschr. v. Ent.*, 77: 230.

Genotype: *Nilobezzia armata* Kieffer, loc. cit. (By monotypy.)

GENERIC CHARACTERS.

The wing venation in *Nilobezzia* is similar to that of *Bezzia*. However, the fourth tarsal segments are subcylindrical and the femora lack stout spines but have some of the setae of the four posterior legs strengthened into spinules. As in the species described below, only one or two such spinules may be present at the distal extremity

of the femora and might easily be overlooked. The tarsi have their fifth segments armed with strong spines and the female claws are equal and barbed.

NILOBEZZIA WHARTONI, n. sp.

Types: Holotype ♀, allotype ♂ and one ♀ paratype in the C.S.I.R. Museum.

Type Locality: All specimens from Fairfax Harbour, Port Moresby, Papua (30.v.1947, R. H. Wharton).

DISTINCTIVE CHARACTERS.

This species may be distinguished from all other species recorded from the region on generic characters alone.
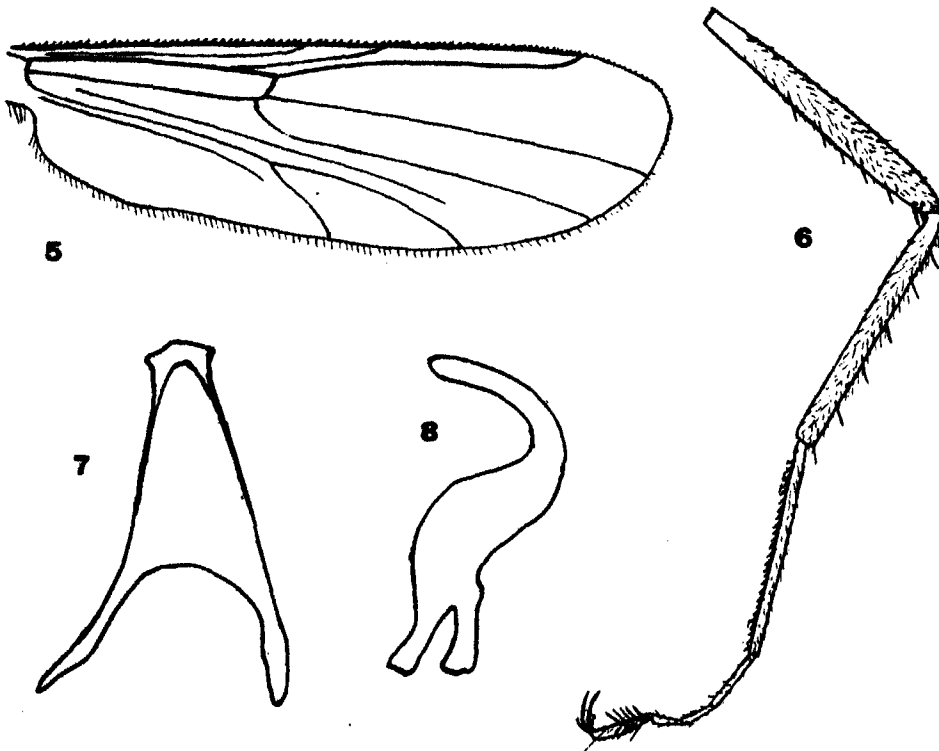
Text-figures 5-8.—*Nilobezzia whartoni.* 5 and 6 from holotype female. 7 and 8 from allotype male. 5, Wing × 35. 6, Hind leg, × 35. 7, Phallosome, × 314. 8, Harpes, × 314.

DESCRIPTION.

Female.

A brown to dark brown species with white halteres, whitish abdomen and brown legs, of which the first four tarsal segments are paler than the rest of the legs.

Head: The head is dark brown, with brown antennae and light brown mouthparts which are scarcely half the height of the head. Of the antennal segments 3 is longer than 4, 4-10 are barrel-shaped, 11-15 elongate and approximately equal, each being about twice the length of 10. The palpi are without any obvious modifications, the third segment is the longest and the fourth and fifth equal. The eyes meet dorsally.

Thorax: The scutum, pleura and postnotum are brown, but the scutellum is a paler brown than the rest of the thorax. The halteres are white with pale yellowish stems.

Legs: The legs are brown with femora, tibiae and fifth tarsal segments darker than the first four tarsal segments. All the femora have one or two thickened spines near the apex and the tibiae have about five similarly stout spines equally spaced along their

whole length. There is, however, only a slight difference between the strength of these spines and the rest of the setae uniformly covering the femora and tibiae. The fourth tarsal segment is the shortest, but is cylindrical. The fifth tarsal segments are elongate, slightly expanded apically and bearing about ten strong pointed spines. The claws are equal, each about as long as the fifth tarsal segment and with a strong basal tooth. Text-fig. 6 illustrates the hind leg.

Wings: The wings are without macrotrichia and the microtrichia are so fine they are scarcely discernible at a magnification of 60 times. The venation is as shown in Text-fig. 5.

Abdomen: The abdomen is yellowish white with somewhat darker areas, particularly at the margins of the tergites and the first tergite is dark brown.

Male.

This sex is noticeably smaller than the female and darker in colour. The thorax is dark brown and the scutellum and postnotum particularly dark. The femora, tibiae and fifth tarsal segments of all legs are dark brown and the rest of the tarsal segments light brown. The claws are small, equal and simple with merely a basal angle. (See Table 1 for measurements of wings and leg segments.) The abdomen is similar to that of the female.

Male Genitalia: The coxites are small and rather narrow (both styles are missing in the allotype), the ninth sternite large, longer than the coxites and complicated with folds and lobes in its distal half. The phallosome is shown in Text-fig. 7 and the fused harpes in Text-fig. 8.

Distribution: As yet this species is only known from the type locality.

References: Any citations not given in full will be found in Part I of this series.

EXPLANATION OF PLATE XXI.

Fig. 5.—Wing of holotype male of *Bezzia tasmaniensis*. × 50.

AUSTRALASIAN CERATOPOGONIDAE (DIPTERA, NEMATOCERA).

PART IV. THE STILOBEZZIA GROUP OF GENERA.

By David J. Lee, B.Sc.

(With Plate xxii and 23 Text-figures.)

[Read 29th October, 1947.]

Introduction.

Three genera of the *Stilobezzia* group have been recognized in the Australasian region, namely, *Stilobezzia* (eight species), *Monohelea* (eight species) and *Acanthohelea* (one species). All the recorded species, of which five out of a total of seventeen are described as new below, come from either New Zealand, Tasmania or New South Wales, with the exception of one species from southern Western Australia. More species will undoubtedly be added to this list and the absence of any records of the group from New Guinea should not be taken as indicative of its absence there since *Stilobezzia* occurs in the Oriental region and on certain islands of the central Pacific and will almost certainly be found in the tropics of the Australasian region when more intensive collecting is undertaken.

For characterization of the group and differentiation of the genera see discussion and key in Part I of this series.

Genus Stilobezzia Kieffer.

Kieffer. J. J., 1911.—*Rec. Indian Mus.*, 6: 118.
   Synonymy: *Hartomyia* Malloch, J. R., 1915. *Bull. Ill. Sta. Lab. Nat. Hist.*, 10: 339.
   Genotype (by original designation): *S. notata* (de Meij.) = *S. festiva* K.

GENERIC CHARACTERS.

Usually of moderate to large size, members of the genus *Stilobezzia* are rather slender insects with few body hairs; the legs are slender and there are no spines on the femora. The female antennae have segments 3–10 oval and 11–15 long and cylindrical, but in the male only the last three or four segments are elongated and there are well developed plumes on the basal segments. Humeral pits are present but may be inconspicuous and the scutum is usually bare of long bristles. The fourth tarsal segment is cordiform, the fifth is not enlarged and the female claws are large and very unequal; an empodium is absent. The wings are rather long with distinct microtrichia over all the surface and usually some macrotrichia at the wing tip. The costa extends to at least two-thirds of the wing length, the two radial cells are very distinct but the second is considerably longer than the first. There is a distinct intercalary fork and the median fork is very obviously petiolate.

Key to Australasian Species of Stilobezzia.

1. Anterior four legs of female with a pair of black spinules at the base of each fifth tarsal segment; all tibiae mottled with numerous dark brown spots, fore femora with two brown bands, mid and hind femora with one brown band .... *pictipes* K.
   No such black spinules on fifth tarsal segments; ornamentation of legs otherwise 2
2. First hind tarsal segment with a basal spine ...., 3
   First hind tarsal segment without a basal spine 4
3. Very dark brown species; scutellum very dark brown. Second radial cell 1·1·5 × first
   .... *antipodalis* I. & M.
   Lighter brown to golden; scutellum yellow. Second radial cell 3 × length of first ....
   .... *tasmaniensis*, n. sp.

AA

DISTINCTIVE CHARACTERS. (See Table 1 for measurements.)

The ornamentation of this species is very characteristic. The fore femora have dark brown bands at about one-third and two-thirds from the base and the mid and hind femora a single preapical dark band (this is at variance with the original description of the hind femora). All tibiae are extensively mottled with dark brown irregular spots and their apices are dark. The abdomen is ornamented, the tergites being dark brown but enclosing an anterior medial pale area on each segment (see Text-fig. 12). There are three very unequal spermathecae (Text-fig. 13), the largest 120μ by 75μ, the next 45μ by 40μ and the smallest 10μ by 10μ.

The original description does not mention the apical spine on the first tarsal segment of the fore leg nor the single basal and two apical spines on the first tarsus of the mid leg and two apical spines on the second tarsal segment. These spines are found in both sexes. The wing is illustrated in Plate xxii, fig. 1.

DESCRIPTION.

Allotype Male.

The male is very similar in colouration to the female. The antennae have segments 3–12 with long dense plumes, segments 4–11 are short, 12 is about twice the length of 11 and 13–15 are about twice the length of 12. The claws are equal, shorter than the fifth tarsal segment; each has a small basal angle and under high magnifications each claw may be seen to be divided at the tip.

Genitalia (see Text-fig. 14): The coxites are complicated by a broad, hook-like basal lobe. The phallosome comprises two converging narrow chitinous rods and the harpes are separate stout rods with recurved tips.

Distribution: I have examined a considerable series of both sexes of this species from Northwood, New South Wales (2.xi.1932, A. R. Woodhill), and from these the allotype was selected. Additional material has been lodged in both the C.S.I.R. and Macleay Museums.

STILOBEZZIA TASMANIENSIS, n. sp.

Types: Holotype ♀ and allotype ♂, together with two ♀♀ paratypes in the C.S.I.R. Museum.
Type Locality: Burnie, Tasmania (31.i.1923, A. Tonnoir). All type specimens with same collection data.

DISTINCTIVE CHARACTERS.

This species is only likely to be confused with *S. antipodalis* which is, however, a much darker species with a very dark brown scutellum as compared with a yellow scutellum in *S. tasmaniensis.* Further, the male genitalia of the two species are quite distinct.

DESCRIPTION. (For measurements see Table 1.)

Female.

Head: The head is brown, shining, with dark bristles on the vertex and overhanging the eyes and including one longer one projecting between the eyes, which are separated by a very narrow space. The antennae are darker brown with the first eight flagellar segments cylindrical and the last five much elongated and all segments have brown hairs. The palpi are short with the segments not obviously modified (Text-fig. 6), although there is a sensory pit towards the distal end of the third segment.

Thorax: The scutum is dark brown, shining with an extensive square golden to golden-brown area at each anterior corner and a light brown prescutellar area. There is a longitudinal row of black hairs along the mid-line and two similar lateral lines on each side, the latter being marked by lighter brown lines on the integument. There are also two pairs of dark, fine spines on the anterior border of the scutum half-way between the middle and the lateral margin and a group of stronger bristles above the wing roots. Humeral pits are present but inconspicuous. The scutellum is yellow with one long dark brown border bristle at the centre and three lateral ones on each side, together with sparse fine hairs. The postnotum is dark brown, the halteres brown at the base with the rest pale yellowish and the pleura have the same range of colour as the scutum.
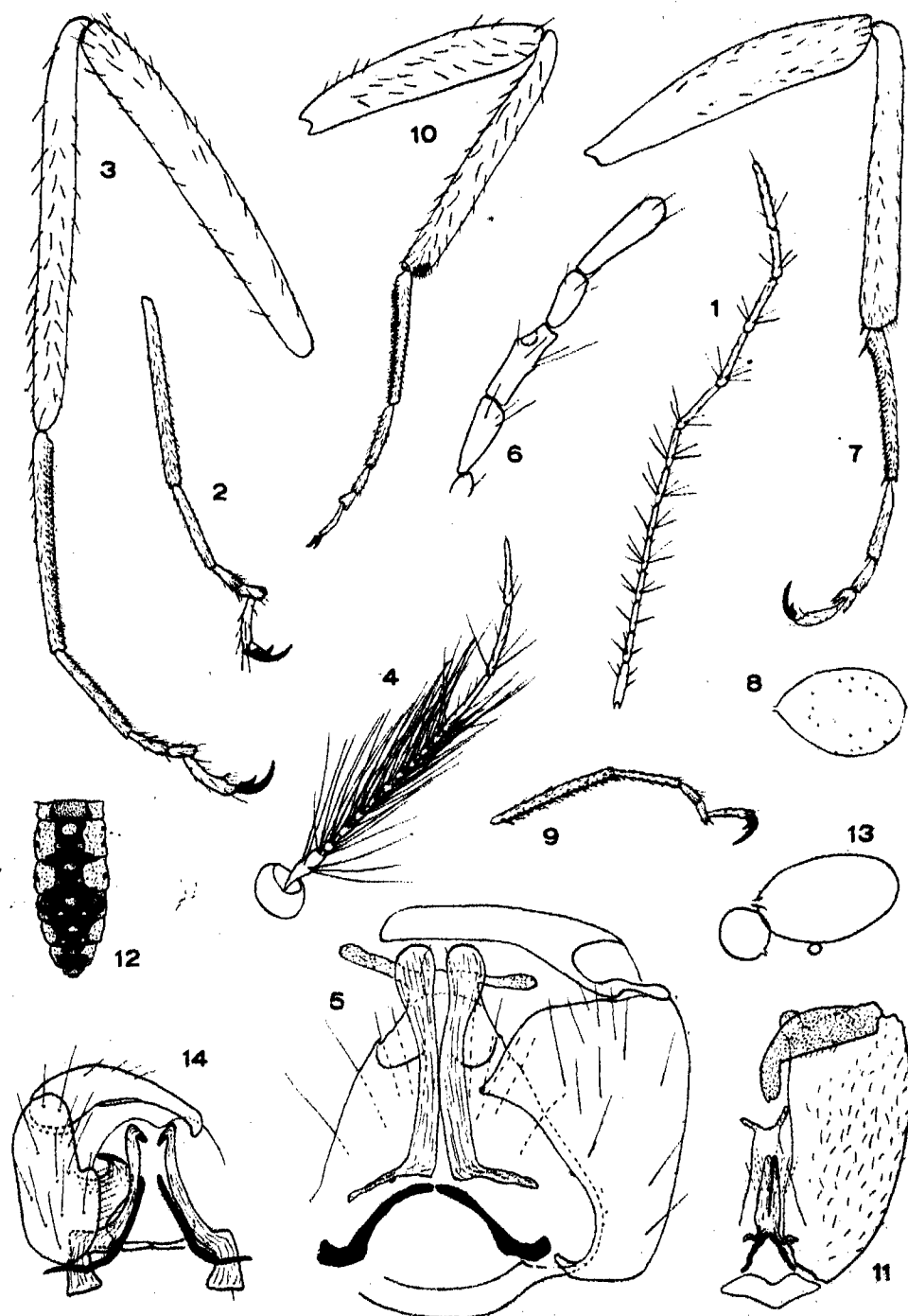
Text-figures 1-14.   Various species of *Stilobezzia*.

Figs. 1-3.—*S. fitzroyensis* (holotype).   1. Antenna (segments 3-15), × 50.   2. Fore tarsus,
× 50.   3. Hind leg, × 50.

Figs. 4-9.—*S. tasmaniensis*, 4 and 5 of allotype male, 6 to 9 of a female paratype.
4. Antenna, × 50.   5. Genitalia, × 160.   6. Palpus, × 160.   7. Hind leg, × 50.   8. Intermediate
spermatheca, × 160.   9. Fore tarsus, × 50.

Legs: The legs are yellowish to golden-brown with the tips of the femora and the third to fifth tarsal segments darker, but there are no pronounced markings. The fourth tarsal segments are bilobed beneath and all the claws are almost as long as the fifth tarsus, single, curved and with a small tooth at the base.

There is a small strong spine at the anterior end of each first tarsal segment and a similar, but less conspicuous spine at the posterior extremities of both the first and second tarsal segments. Both the fore tarsus and the hind leg are figured (Text-figs. 9 and 7).

Wings: There are distinct microtrichia all over the wings (see Plate xxii, fig. 4), but macrotrichia are present at the tip only. The radial cells are well formed, the second three times as long as the first and the costa extends over two-thirds of the wing length.

Abdomen: This is brown with a yellowish tip and there is a group of black bristles at the sides of the first abdominal segment. The spermathecae are three in number, all unequal, and the smallest is minute. All have a short chitinized duct and all are sparsely pitted. The smaller of the two large spermathecae is shown in Text-fig. 8. The dimensions of the spermathecae are 120μ by 85μ, 100μ by 70μ and 30μ by 20μ.

Male.

This sex is similar to the female in colouration and bristling. All the antennal segments (Text-fig. 4) are dark brown and there are long plumes on segments 3–12, but only 13–15 are elongate. All the tarsal claws are equal and simple and the wings have only a very few macrotrichia at the tip.

The genitalia (Text-fig. 5) are well developed with broad coxites and unmodified styles. The ninth tergite is as long as the coxites, and terminates distally in two divergent finger-like processes and the harpes are almost as long as the coxites, lying close together, of uniform width for most of their length but a little swollen distally. The phallosome consists of two curved rods almost uniting distally.

Distribution: Apart from the type series I have seen one other male from Cradle Valley, Tasmania (A. Tonnoir, 26.i.1923).

STILOBEZZIA GENITALIS, n. sp.

Type: Holotype ♂ in the C.S.I.R. Museum.
Type Locality: Strahan, Tasmania (6.ii.1923, A. Tonnoir).

DISTINCTIVE CHARACTERS.

This species is very similar in general colouration to *S. tasmaniensis* but the first tarsal segment lacks a basal spine (which would no doubt serve to distinguish females) and the genitalia are relatively enormous, each coxite measuring 0·85 by 0·34 mm.

DESCRIPTION. (For measurements see Table 1.)

Male.

The measurements of the antennae, legs and wings closely parallel those of *S. tasmaniensis*. The scutum has a square golden area at the anterior corners only and the pleura are almost as light as these areas. The scutellum has one central border bristle with four laterals on each side. The first tarsal segments lack a strong basal spine. (See Text-fig. 10 for illustration of hind leg.) The wing is illustrated in Plate xxii, fig. 2.

The genitalia (Text-fig. 11) have greatly enlarged coxites each of which has a thumb-like process on the inner side and the styles are very heavily chitinized and finely hairy with the tip strongly bent. The ninth tergite is only about half the length of the coxite

Figs. 10–11.—*S. genitalis*. 10. Hind leg of holotype, × 50. Genitalia of specimen from Cradle Valley, × 50.
Figs. 12–14.—*S. pictipes* (specimens from Northwood). 12. Dorsum of female abdomen, × 20. 13. Spermathecae, × 160. 14. Male genitalia, × 160.

and terminates in two divergent finger-like processes. The harpes are elongate simple structures lying side by side and the phallosome consists of two separate short rods almost meeting apically but widely divergent at the base.

The female is not yet known.

Distribution: I have examined a further male of this species from Cradle Valley, Tasmania (A. Tonnoir, 19.i.1923).

STILOBEZZIA FITZROYENSIS, n. sp.

Type: Holotype ♀ in the C.S.I.R. Museum.
Type Locality: Fitzroy Falls, New South Wales (22-27.xi.1937, A. Tonnoir).

DISTINCTIVE CHARACTERS.

A large, rather dark brown species with largely pale legs in which the first tarsal segments lack a basal spine. The second radial cell is four times the length of the first and the distal part of R_1 is in line with r-m.

DESCRIPTION. (For measurements see Table 1.)

Female.

Head: The head is chestnut brown with a row of black orbital bristles above the eyes but otherwise it is bare dorsally. The eyes are separated by only a fine line. The antennal segments are cylindrical with the last five elongate (Text-fig. 1).

Thorax: The thorax is rather darker brown than the head, with a dull brownish bloom. The pleura are similarly dark brown but the scutellum is distinctly paler (reddish-brown) and invested with some nine dark bristles. Humeral pits are obvious and the scutum is largely bare with a few bristles just above the wing roots and just anterior to the scutellum. The halteres are yellowish.

Legs: The legs are generally pale yellowish with the fourth and fifth tarsi darker and the apices of the first tarsal segments are also narrowly dark and the femora reddish-brown. The fourth tarsal segment is bilobed beneath (in Text-figs. 2 and 3 it is shown in lateral view, hence it does not appear bilobed in these illustrations).

Wings: The wings (Plate xxii, fig. 3) are entirely clothed with microtrichia and macrotrichia are numerous on the distal portion of the wing from the level of the end of the costa to the tip and the intercalary fork is distinct.

The second radial cell is four times the length of the first and r-m and the distal part of R_1 are in line.

Abdomen: The abdomen is greyish-brown, sparsely clothed with short hairs and there are two large and one minute spermathecae, all of which are sparsely pitted. The two large spermathecae measure 95μ by 70μ and 85μ by 65μ.

Distribution: Only known from the type locality.

Genus MONOHELEA Kieffer.

KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15: 294 and 312.
Synonymy: *Schizohelea*[*] Kieffer, J. J., 1917. *Ann. Mus. Nat. Hung.*, 15: 295. *Allohelea* Kieffer, J. J., 1917. *Ann. Mus. Nat. Hung.*, 15: 364.
Genotype: *M. hieroglyphica* Kieffer 1917, loc. cit. (by original designation).

GENERIC CHARACTERS.

This genus resembles *Stilobezzia* in most respects but differs particularly in the characters of the fourth tarsal segment and the female claws.

The body is not very hairy and rather shorter than in *Stilobezzia*. The fore and mid legs are unmodified, the fourth tarsal segment is short but cylindrical and the tarsal claws are relatively small and equal in both sexes. In the hind legs both the femora and the tibiae may be normal or somewhat enlarged but the femora are without spines although strong hairs may be present; tarsus I has a strong spine at the tip and there is one very long claw (equalling the fifth tarsal segment in length) with a basal spine. In the male all the claws are equal and simple and no empodium is present in either sex. In both sexes the combined length of the femora and tibiae appears disproportionately

---

[*] Edwards (1926) suggests that the name *Schizohelea* has priority over *Monohelea*. Reference to the pagination cited above clearly indicates that this suggestion is erroneous.

long in relation to the tarsal length and the first hind tarsal segment may be slightly curved at the base. At most there are a few macrotrichia at the wing tip and the microtrichia are very fine and can only be discerned at high magnifications. The costa extends well beyond the middle of the wing and of the two radial cells the second is often distinctly longer than the first. The median fork is petiolate and M_2 continuous without any basal interruption.

In the two species of which I have examined males there are certain common features in the genitalia. The ninth tergite is broad, even apically, with the distal margin broadly indented and there are two small hairy lobes on the inner surface. The phallosome is complicated by an accessory chitinized structure lying between it and the harpes. Whether these characters are typical of the genus as a whole remains to be determined although the phallosome of *M. antipodalis*, as figured by Ingram and Macfie (1931), appears to be simple.

TABLE 1.

Various Measurements of Species of Stilobezzia and Monohelea.

	Stilo-bezzia fitzroy-ensis ♀	Stilo-bezzia tasmani-ensis ♀	Stilo-bezzia tasmani-ensis ♂	Stilo-bezzia genitalis ♂	Stilo-bezzia pictipes ♀	Mono-helea tasmani-ensis ♀	Mono-helea tasmani-ensis ♂	Mono-helea brevipes ♂	Mono-helea tigrinus ♀
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Wing—									
Length ..	3·0	2·295		2·278	1·921	1·94		2·47	0·935
Width ..	1·0	0·748		0·607	0·714	0·68		0·60	0·289
Antenna—									
Total length segments 3–15	1·73	1·275	1·100	1·245	1·190				
Segment 3 ..	0·145	0·095	0·160	0·150	0·100	0·055			0·030
„ 4 ..	0·095	0·055	0·060	0·055	0·060	0·040			0·020
„ 5 ..	0·095	0·055	0·060	0·055	0·065	0·040			0·023
„ 6 ..	0·090	0·055	0·055	0·055	0·065	0·040			0·025
„ 7 ..	0·100	0·055	0·050	0·050	0·065	0·045			0·025
„ 8 ..	0·100	0·060	0·045	0·050	0·065	0·045			0·025
„ 9 ..	0·115	0·080	0·045	0·045	0·065	0·045			0·030
„ 10 ..	0·115	0·070	0·040	0·045	0·075	0·055			0·030
„ 11 ..	0·175	0·080	0·045	0·050	0·140	0·085			0·035
„ 12 ..	0·175	0·165	0·050	0·050	0·155	0·080			0·040
„ 13 ..	0·165	0·160	0·200	0·250	0·155	0·090			0·040
„ 14 ..	0·150	0·150	0·200	0·200	0·155	0·090			0·040
„ 15 ..	0·210	0·160	0·190	0·190	0·185	0·100			0·055
Palpus—									
Segment 2 ..		0·065			0·075	0·045			0·030
„ 3 ..		0·075			0·075	0·085			0·030
„ 4 ..		0·050			0·055	0·050			0·023
„ 5 ..		0·100			0·060	0·065			0·045
Fore leg—									
Femur.. ..	0·884	0·680			0·629	0·510		0·714	
Tibia	0·901	0·680			0·561	0·510		0·680	
Tarsus I ..	0·527	0·374			0·374	0·204		0·272	
„ II ..	0·255	0·187			0·170	0·119		0·187	
„ III ..	0·085	0·085			0·059	0·085		0·136	
„ IV ..	0·068	0·068			0·051	0·060		0·085	
„ V ..	0·170	0·136			0·102	0·119		0·136	
Claw	0·119	0·102			0·102	0·051		0·041	
Hind leg—									
Femur.. ..	1·020	0·884	0·901	0·731	0·646	0·850	0·731	1·156	0·430
Tibia	1·071	0·867	0·867	0·782	0·765	0·850	0·731	1·224	0·410
Tarsus I ..	0·595	0·442	0·442	0·374	0·425	0·289	0·289	0·340	0·175
„ II ..	0·306	0·221	0·238	0·187	0·170	0·204	0·187	0·187	0·085
„ III ..	0·102	0·102	0·102	0·085	0·051	0·119	0·119	0·136	
„ IV ..	0·078	0·068	0·051	0·051	0·034	0·102	0·085	0·102	
„ V ..	0·170	0·136	0·102	0·119	0·068	0·136	0·136	0·187	
Claw	0·119	0·101	0·043	0·043	0·068	0·187	0·043	0·068	

Key to Australasian Species of Monohelea.

1. Wings ornamented with dark spotting .... *nubeculosa* Macfie
   Wings not ornamented 2
2. Wing length only about 1·0 mm., small species .... *tigrinus* (Sk.)
   Wing length about 2·0 mm. or more, larger species 3
3. First hind tarsal segment with strong spine at base only .... *tonnoiri* Macfie
   First hind tarsal segment with strong spines at both base and apex but none at centre .. 4
   First hind tarsal segment with strong spines at base, middle and apex 6
4. Legs uniformly brown .... *tasmaniensis*, n. sp.
   Legs with dark bands apically on hind tibiae 5
5. Less robust species, with dark band on hind femur occupying distal third .. *ferruginea* Macfie
   Very robust species, with dark band on hind femur only occupying distal fifth; very strong
       series of nine spines at apex of hind tibia .... *brevipes*, n. sp.
6. Dark band on hind femur extending to apex .... *clavipes* Macfie
   Dark band on hind femur not reaching apex .... *antipodalis* I. & M.

MONOHELEA NUBECULOSA Macfie.

MACFIE, J. W. S., 1932.—*Ann. Trop. Med. and Parasit.*, 26 : 45.
   Type: ♀ type in British Museum (Natural History).
   Type Locality: Lake Brunner, New Zealand.

MONOHELEA TONNOIRI Macfie.

MACFIE, J. W. S., 1932.—*Ann. Trop. Med. and Parasit.*, 26 : 46.
   Type: ♀ type in British Museum (Natural History).
   Type Locality: Nelson, New Zealand.

MONOHELEA CLAVIPES Macfie.

MACFIE, J. W. S., 1932.—*Ann. Trop. Med. and Parasit.*, 26 : 48.
   Type: ♀ type in British Museum (Natural History).
   Type Locality: Dun Mt., New Zealand.

MONOHELEA FERRUGINEA Macfie.

MACFIE, J. W. S., 1932.—*Ann. Trop. Med. and Parasit.*, 26 : 49.
   Type: ♀ type in British Museum (Natural History).
   Type Locality: Waiho, New Zealand.

MONOHELEA ANTIPODALIS Ingram and Macfie.

INGRAM, A., and MACFIE, J. W. S., 1931.—*Ann. Trop. Med. and Parasit.*, 25 : 205.
MACFIE, J. W. S., 1932.—*Ann. Trop. Med. and Parasit.*, 26 : 44 (in key).
   Types: Type ♂♂ in British Museum (Natural History).
   Type Locality: Ohakune, New Zealand.

MONOHELEA TIGRINUS (Skuse).

SKUSE, F. A., 1889.—PROC. LINN. SOC. N.S.W., 4 (2nd series) : 306 (*Ceratopogon*).
KIEFFER, J. J., 1917.—*Ann. Mus. Nat. Hung.*, 15 : 191 (*Stilobezzia*).
   Type: Holotype ♀ in Macleay Museum, University of Sydney.
   Type Locality: Berowra, New South Wales.
   Synonymy: *Ceratopogon tigrinus*, Skuse 1889, loc. cit. *Ceratolophus tigrinus*, Kieffer, J. J.,
1906. Chironomidae in Wytsman's Genera Insectorum, fasc. 42 : 61. *Stilobezzia tigrinus*,
Kieffer 1917, loc. cit.

   Note: Skuse's type (mounted in gum on a card) was not satisfactory for critical examination
so the specimen was soaked off in water and remounted in euparal. Sufficient can now be
seen to place this species, at least tentatively, in the genus *Monohelea* and there should be little
difficulty in recognising this species when it is taken again in the field even though complete
redescription is not possible.

DISTINCTIVE CHARACTERS.

The small size of this species is alone sufficient to differentiate it from any of the
other known species of *Monohelea* in the region. The various measurements are given
in Table 1.
   The relevant part of the original description, concerning characters which can no
longer be distinguished in the type, are as follows: "Antennae, clypeus and palpi black.
Thorax brown, dull, with two longitudinal stripes and three irregular lateral spots of
ochreous; sparingly covered with short brown hairs; pleurae, pectus, and metanotum
dark brown; scutellum light brown. Halteres brown. Abdomen short, robust, dusky

16 15 22 19 21 20 18 17 23
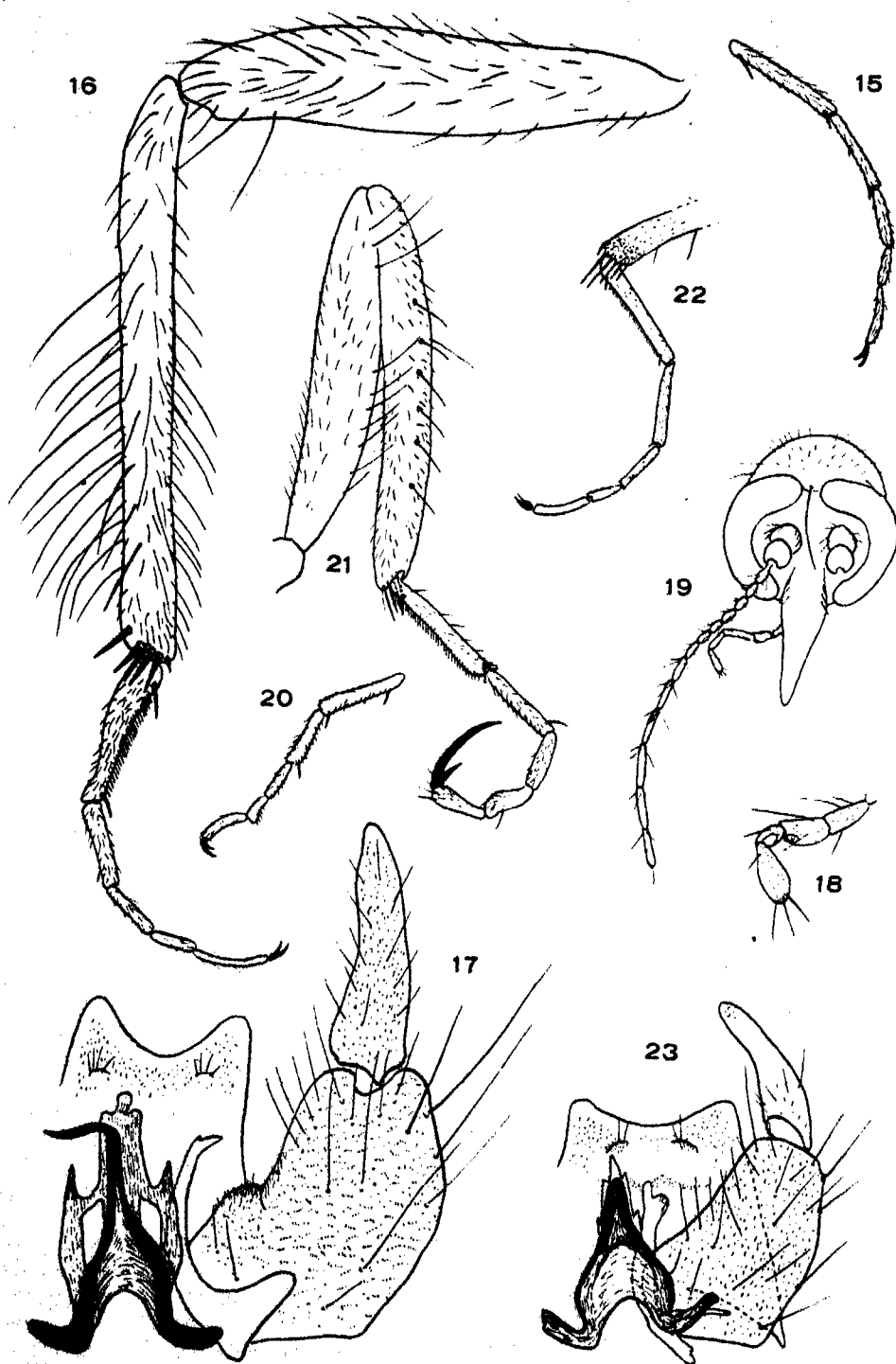
Text-figures 15-23. Various species of *Monohelea*.

Figs. 15-17. *M. brevipes* (holotype male). 15. Fore tarsus, × 66. 16. Hind leg, × 66.
17. Genitalia, × 134. 18. *M. tigrinus* (holotype female), palpus, × 200.

Figs. 19-23. *M. tasmaniensis*. 19 to 21. Holotype female. 22 and 23. Allotype male.
19. Anterior view of head, × 66. 20. Fore tarsus, × 66. 21. Hind leg, × 66. 22. Hind tarsus,
× 66. 23. Genitalia, × 134.

brown, clothed with brown hairs. Legs brown, tips of femora and tarsi yellowish; posterior tibiae incrassated. In fore legs tibia somewhat more than twice length of metatarsus. . . ."

In addition to these characters the following can be seen in the mounted type. The antennal segments are subcylindrical with the apical five only a little longer than the preceding ones and there appears to be a long spine arising from the frons. The segments of the palpi are as illustrated in Text-fig. 18. The hind tibia is over twice the length of tarsus I and the tarsal ratio is 2·0. In addition the hind first tarsus bears a basal spine and the segment is rather bent at the base. There are spines at the apex of the hind tibia and the claws are all rather long, equal on the anterior four legs but single on the posterior legs (whether or not there is a basal spine cannot be discerned). On the wings the first radial cell is two-thirds the length of the second radial cell (see Plate xxii, fig. 7).

Distribution: This species is still only known from the type locality.

MONOHELEA TASMANIENSIS, n. sp.

Types: Holotype ♀, allotype ♂ together with one ♀ and one ♂ paratypes in the C.S.I.R. Museum.

Type Locality: Cradle Valley, Tasmania (A. Tonnoir, 16.i.1923). All type specimens with same collection data.

DISTINCTIVE CHARACTERS.

This species must be extremely close to *M. tonnoiri*. Apart from the slight differences in the measurements of antennal segments, the only obvious character which may serve to distinguish the two is the presence of a spine at the distal end of tarsus I in *M. tasmaniensis* instead of only a basal one as in *M. tonnoiri*. The discovery of the male of the latter species would probably make it possible to establish the relationship of the two species.

DESCRIPTION. (See Table 1 for measurements.)
Female.

Head: The head is greyish dorsally with dark brown bristles; the eyes are just separated with a long, strong, fine spine arising on the frons and projecting down between the bases of the antennae (see Text-fig. 19). The latter are dark brown, the first eight flagellar segments are short and oval, the last five elongated and cylindrical. The segments of the palpi are cylindrical, the third being about twice as long as the second and a little longer than the fourth and fifth.

Thorax: The scutum is dark brown with a greyish pubescence, lighter brown at the anterior corners with a sparse covering of long brown hairs which are longest at the lateral margins and in front of the scutellum. The humeral pits are well developed. The scutellum is brown at the centre and light brown laterally with about four long border bristles on each side and a scattering of short hairs. The postnotum is dark with greyish pubescence, the halteres are yellowish-white and the pleura similar to the scutum.

Legs: The legs have the mid and hind coxae similar in colour to the pleura but the fore coxae are yellowish-brown; the rest of the legs are yellowish-brown. The hind femora are somewhat swollen, with some long hairs but no spines and the hind tibiae are similarly clothed but with a row of about six spine-like hairs, and there is also a comb of five strong spines (two of which are longer than the other three) at the apex. There is a stout spine at both the base and the apex of the first tarsal segment of all the legs, the fourth tarsal segment is subcylindrical, the fifth is unarmed and the claws of the anterior four legs are equal and small, but those of the hind legs are very long, single and with a basal tooth (see Text-figs. 20 and 21 for illustration of fore tarsus and hind leg).

Wings: The wings (Plate xxii, fig. 5) have very fine microtrichia, only visible at high magnifications and a few macrotrichia on the apical portion only. The costa extends to about two-thirds of the wing length, the radial cells are distinct, the first

Abdomen: This is similar in colour to the thorax, clothed with sparse but prominent hairs and in length it is about twice that of the thorax.

Genitalia (Text-fig. 17): The phallosome is strongly recurved at the tip and there is a complex accessory structure between it and the harpes and the latter are strongly chitinized with an unequally bidentate apex.

Distribution: Only known from the type locality.

Genus ACANTHOHELEA Kieffer.

KIEFFER, J. J., 1917.—*Ann. Nat. Mus. Hung.*, 15: 198.
Genotype (by monotypy): *A. pruinosa* Kieffer, loc. cit.

GENERIC CHARACTERS.

This genus belongs to the *Stilobezzia* group of genera and may be recognized by the presence of microtrichia on the wings, the petiolate median stem, both radial cells open, bilobed fourth tarsus on all legs and all femora and tibiae spinose.

ACANTHOHELEA PRUINOSA Kieffer.

KIEFFER, J. J., 1917.—*Ann. Nat. Mus. Hung.*, 15: 198.
Type: Type ♂ presumably in National Museum of Hungary, Budapest.
Type Locality: Sydney, New South Wales.

Translation of Original Description.

"♂. Reddish yellow, dull and pruinose. Head seen from before circular. Mouthparts brownish-black, slender and long, longer than the height of the head. Eyes glabrous, confluent at the vertex. Palpi black, very long, 5-segmented, of which the third is a little longer than the fifth, not enlarged, fourth distinctly shorter than the fifth, the latter without long hairs. Antennae 15-segmented, plume golden yellow, reaching segment 14, scape reddish-brown, segments 3-12 yellow, 13-15 brownish black, segments 4-12 cylindrical, distinctly longer than wide, the three last segments are elongated, filiform, each three times as long as 12, 13 and 14 have a long verticel at their base. Thorax higher than long, convex, without spinule in front, glabrous, save several hairs on the scutellum and on the sides of the mesonotum. Halteres brown, extremity of the club whitish. Wings subhyaline, lobed, glabrous, with two indistinct brownish spots, one on r-m, the other at the beginning of the anterior branch of the intercalary fork, the latter distinct but finer than the other veins, R$_{4+5}$ reaching the distal third of the wing, not exceeded by the costa, twice as long as R$_1$, its base very oblique and shorter than r-m, base of Cu$_1$ under r-m, M$_{3+4}$ continuing the direction of the stem, Cu$_1$ very oblique, anal not bifurcated. Legs brownish-black, not enlarged, the two anterior reddish-yellow, segments I-III of all the tarsi whitish, fourth and fifth black; posterior legs a little larger and longer than the anterior four, all the femora are armed with short spines, not only on their ventral part, but on all their periphery, tibiae with similar spines but longer and sparser, tarsi distinctly longer than the tibiae, posterior first tarsi as long as the two following segments together, third segment more than three times as long as wide, anterior first tarsus longer than the two following segments together, fourth segment of all the tarsi transverse, cordiform, prolonged in two lobes below, fifth slender, at least as long as the third, curved and inermous; claws of moderate length, equalling one-third of the segment, equal and simple. Abdomen brownish-black, a little clearer dorsally at the front, feebly haired, one-half longer than the rest of the body, very much narrower than the thorax, subcylindrical; hypopygium large, wider than the abdomen, terminal segments very slender. Length 3·5 mm."

This species has not since been taken in the Sydney district, but there should be little difficulty in recognizing it from the spinose femora and tibiae. It should be noted that Macfie (1940), in his key to the *Stilobezzia* group, presumes in couplet 2 that the claws of the female are similar to those of *Stilobezzia*. Since the female of the genotype, *A. pruinosa*, is not known, this presumption is scarcely justified and the use of this key for the recognition of *Acanthohelea* may prove misleading.

References.

See Part 1 of this series for any references to literature not cited in full in the text.

EXPLANATION OF PLATE XXII.

Figs. 1-7. Wings of various species of *Stilobezzia* and *Monohelea*. All × 23. 1. *S. plotipes* (female specimen from Northwood). 2. *S. genitalis* (male specimen from Cradle Valley). 3. *S. fitzroyensis* (holotype). 4. *S. tasmaniensis* (paratype female). 5. *M. tasmaniensis* (holotype). 6. *M. brevipes* (holotype). 7. *M. tigrinus* (holotype).

SIMULIIDAE (DIPTERA, NEMATOCERA) FROM NEW GUINEA, WITH THE DESCRIPTION OF ONE NEW SPECIES.

By R. H. WHARTON, B.Sc., Department of Zoology, University of Sydney.

(Twenty-three Text-figures.)

[Read 26th November, 1947.]

INTRODUCTION.

Three species of Simuliidae have been described from New Guinea, all by Enderlein (1922, 1936), from specimens collected by Biro in 1898 and 1900. Each species was assigned to a different genus by Enderlein, but Smart (1945) included all three in the genus *Simulium* Latreille. One of these species may now be regarded as a synonym of *S. ornatipes* Skuse, a species known to be widely distributed in Australia, and here recorded for the first time from New Guinea. A new species of *Simulium* is described, found breeding with *S. ornatipes* at Port Moresby. No adults of either species were collected but were obtained from pupae kept on moist cotton-wool.* Also included are translations of the original descriptions of Enderlein's two species and an attempt is made to clarify their systematic position.

SIMULIUM ORNATIPES Skuse.

SKUSE, F. A., 1890.—*Proc. Linn. Soc. N.S.W.*, (2) 5: 632.
TONNOIR, A. L., 1925.—*Bull. ent. Res.*, 15: 232.
DRUMMOND, F. H., 1931.—*J. R. Soc. W. Aust.*, 18: 6.

Synonymy: *Chelocnetha biroi* Enderlein, G., 1936. *Sitzber. naturf. Freunde*, 1936: 121.
Male and female types placed in either Budapest or Berlin Museum.

Type Locality: Specimens stated to come from Sydney, Australia, 24.11.1900 (see discussion below), collected by L. Biro.

Types: Although Tonnoir (1925) re-examined Skuse's syntype series and selected a lectotype male and allotype female, only the female is labelled as such. These specimens are lodged in the Australian Museum, Sydney.

Type Locality: Darling River, New South Wales.

A revision of the specimens used by Skuse has been carried out by Tonnoir and the immature stages described by Drummond from Western Australian material. Enderlein created a new genus, *Chelocnetha*, with genotype *C. biroi* for specimens, stated to be from New Guinea in the description of the genus, and from Sydney, Australia, in the description of the species, and without reference to the original material it is impossible to say from which of these places the specimens actually came, as the collector visited both regions. Smart (1945) transferred this species to the genus *Simulium*, and now, after examining Enderlein's original description, it is obvious that *S. biroi* is a synonym of *S. ornatipes*. Fortunately, any confusion which could have arisen from Enderlein's geographic error can now be obviated, as the species is known to occur in both places.

Distribution: Specimens have been collected in Western Australia, South Australia, New South Wales, and Queensland. Port Moresby, New Guinea (Lee and Wharton, June, 1947), is a new record, larvae and pupae being found attached to the under surface of stones in a small, fairly rapidly moving stream about 30 feet above sea-level.

---

* The pupae, which were collected on the 6th July, 1947, during the morning, were immediately placed on moist cotton wool in small tins. No adults had emerged by the following day, when the tins were transported by air from Port Moresby to Sydney, New South Wales. When the tins were opened on the 9th July, several adults had emerged and died. The pupae were then kept at a fairly constant temperature (75°F.). Further adults emerged during the following two days.

SIMULIUM OCULATA (Enderlein).

ENDERLEIN, G., 1936.—*Sitzber. Ges. naturf. Freunde*, 1936 : 121.   (*Pselaphochir oculata.*)
SMART, J., *Trans. R. ent. Soc. Lond.*, 95 : 493.

Synonymy : Pselaphochir oculata, Enderlein, 1936.   (Smart, in the world list of Simuliidae, regards *Pselaphochir* as synonymous with *Simulium.*)

Types : Presumably the male and female type specimens are in either the Budapest or Berlin Museum.

Type Locality : Sattleburg, Huon Gulf, New Guinea.

DISTINCTIVE CHARACTERS.

The description of this species is quite inadequate, but the most obvious characters which may be of use in identification are the unusually large upper facets in the male eye, the shape and relative length of the hind tibiae and first tarsi in both sexes, the absence of claws, and the absence of bright scales or hairs on the second abdominal tergite.   No mention is made of any pale area on the first hind tarsi, a character which is of importance in the remaining New Guinea species.

The translation of Enderlein's original generic and specific descriptions is:

"*Pselaphochir*, n. gen."

"*Type* : *P. oculata*, n. sp.   New Guinea."

"*Male and Female* : Female claws toothless.   Metatarsus of hind leg of male flattened and fusiformly broadened. First and third hind tarsi in male and female with two extraordinarily long hairs arising on the outer surface at the apex, each hair as long or longer than the second tarsus.   Macrommatium (upper area of the eye) of the male with unusually large facets, diameter of which is somewhat greater than the diameter of the antennal flagella segments. On the median line between the eyes of the male, a longitudinal row of long hairs."

"R and R$_1$ pubescent, RR (probably Rs) with very short pubescence, in the female Sc is also pubescent."

"The genus *Morops* (Enderl. 1930) (type *M. pygmaea* Enderl. 1922, N.G.) is close to this genus, but differs in the small parallel-like metatarsus of the hind leg of the male and in the sharp angle at the end of the second-third of the hind tibia.   The two remarkably long hairs at the tip of the first and the third fore tarsi occur also in the same way in *Morops.*"

"*Pselaphochir oculata*, n. sp."

"*Female.*   !

"*Head* : Black with light grey bloom and short, metallic-yellow pubescence.   Frons about one and a half times as long as it is broad posteriorly, and about three times as long as it is broad anteriorly."

"*Thorax* : Dull black, with golden-yellow pubescence, particularly on the top.   *Abdomen* : Dull brown, the base slightly brighter in colour.   The last three segments black and rather smooth ; pubescence yellowish, slightly so on the top but denser on the sides ; halteres metallic yellow, stem dark brown.   *Legs* : Brown, base of hind tibia more or less bright yellow on the outside ; first hind tarsus about four-fifths of the tibia, and about two-thirds of its width. *Wings* : Clear, veins brownish-yellow.   Costa brown."

"*Male.*

"Body brown, abdomen dark brown.   Mesonotum with dense golden-yellow hairs.   Posterior margin of the tergites brighter (presumably than the female).   Hind (posterior) bristles of the first tergite yellow-brown.   Legs brown, tip of the femora, basal half of the tibiae with pale yellowish, flat-lying pubescence.   Basal half of hind tibia pale yellowish.   Halteres vivid metallic yellow, stem brown."

"Body Length : Male, 2·25 mm. ; Female, 1·75-2·25 mm.   Wing Length : 2·5-2·75 mm."

"N.G. (Sattleburg, Huon Gulf), Nov., 1898.   Male and Female, L. Biro."

"*Type* : Museum—Budapest and Berlin."

Distribution : Sattleburg, Huon Gulf, New Guinea.   This species has not yet been rediscovered.

SIMULIUM WILHELMLANDAE Smart.

SMART, J., 1944.—*Proc. R. Ent. Soc. Lond.*, (B) 13 : 132.
ENDERLEIN, G., 1922.—*Konowia*, 1 : 70.   (*Wilhemia pygmaea.*)

Synonymy : Wilhemia pygmaea, Enderlein, 1922.

Morops pygmaea, Enderlein, 1930.   *Arch. klassif. phylog. Ent.*, 1 : 93.   (The name *wilhelmlandae* was given to this species by Smart in 1944 when he transferred it to *Simulium*, in which genus *pygmaea* is preoccupied.)

Types and Type Locality : No record of where the type male, collected in "New Guinea, Kaiser Wilhelmland", is lodged.   If still in existence it is probably in either the Budapest or Berlin Museum.

DISTINCTIVE CHARACTERS.

Though the description, based on a single male specimen, is not complete, this species should be easily recognized. The bright brown-yellow antennae and the bright ochreous yellow first two abdominal tergites are sufficient to separate this form from known New Guinea or Australian species. It should be noted that the first hind tarsi are mainly yellow.

The translation of Enderlein's original description follows:

"*Wilhemia pygmaea*, n. sp."

"New Guinea, Kaiser Wilhelmland. One male collected by Hollsong."

"*Male*. Eyes reddish-black. Clypeus grey-black with yellowish outstanding pubescence. Palpi black. Antennae bright brown-yellow."

"*Thorax*: Dull, brown-black, mesonotum with sparse yellow pubescence and with traces of smoothness in the middle (probably a rubbed specimen!). Scutellum dark brown. Metanotum dull black. *Abdomen*: Dull black, slightly smooth above on the sides; pubescence sparse and very short. First and second tergites bright yellow ochre, the long hairs of the first tergite also bright yellow ochre. *Halteres* large, vivid rust-yellow."

"*Legs*: Coxae grey-brown, fore coxae brown yellow. Trochanter brown-yellowish. Femora dark brown, the hind femur flattened and broadly spindle-shaped. Tibiae dark brown, basal fifth bright yellow ochre; fore tibia a very little flattened and broadened, the remainder considerably flattened and broadened, the hind tibia in such a way that a pronounced, almost slightly angular, convexity is formed on the outer margin of the basal half. Tarsi dark brown, the first hind tarsi except for the apical third bright yellow ochre, and with strikingly long and thin, single, outstanding hairs which may be three times as long as the cross-section of the tarsi. First fore tarsus cylindrical, about four-fifths of the length of the tibia; first hind tarsus small, parallel, very slightly flattened and broadened, less than half the breadth of the tibia at the broadest part, and about three-quarters of the length of the tibia."

"*Claws* untoothed—short and fine."

"*Wings* clear, veins C, Sc, and R bright yellow-brown."

"Body length: 1·2 mm. Wing length: 1·3 mm."

Distribution: Merely recorded from New Guinea, Kaiser Wilhelmland. This species has not as yet been rediscovered.

SIMULIUM PAPUENSIS, n. sp.

Types: Pinned holotype female and allotype male, together with one pinned female paratype in the Macleay Museum, University of Sydney. Morphotype larva and pupa, mounted on slides, larval and pupal specimens in alcohol, and one female and two male paratypes mounted on slides, also in the Macleay Museum. One female and one male paratype, pupae and larvae, in the Queensland Institute of Medical Research.

Type Locality: Jackson Strip, Port Moresby, New Guinea (Lee and Wharton, June, 1947.)

DISTINCTIVE CHARACTERS.

This species belongs to an Australasian group of the genus *Simulium* characterized particularly by the presence of a patch of scales on the membranous (prealar) area behind the mesothoracic spiracle. Characters which distinguish *S. papuensis* from Australian members of the group are: (i) *Adult*: The antennae mainly dark; the hind tibia slightly angulated in both sexes, but more accentuated in the male; abdomen with dense silver (sometimes appearing light golden) scales on the posterior margin of the first, and complete covering of similar scales on the second tergite; and the tarsal claws with a small basal tooth in both males and females. (ii) *Pupa*: The dendroid respiratory organs. (iii) *Larvae*: The frontoclypeus with longitudinal pigmented dark band; the pupal gill spots; and each lobe of the anal gills with several finger-like processes.

DESCRIPTION.

Female. Length 2·0–2·3 mm. Wing 2 mm.

Head: The frons, vertex and occiput are dull black and covered with a silver-grey pubescence, the frons between one-quarter and one-third of the maximum width of the head, and about one and a half times as long as wide. The antennae (Text-fig. 1) are composed of eleven segments, of which the basal two and the base of the third are light brown, the remainder being dark brown to black with a fine grey pubescence. There are five segments in the palpi, the basal two small, the third large, slightly

less than twice as long as wide, the fourth not as broad as the third and a little shorter, the fifth longer than the third, but comparatively slender, more than four times as long as broad (Text-fig. 2). The buccal armature is similar to that figured for the male (Text-fig. 9).

Thorax: The mesonotum is black, with scattered fine golden scales. The pleura are bare and dull black, except for a patch of light golden scales on the membranous (prealar) area behind the mesothoracic spiracle, a group of similar scales on the propleuron, and a small group of bristles, which are dark at the roots but may appear pale distally, on the upper mesepimeron. The scutellum has a row of long, black bristles along its posterior margin and scattered golden scales on its dorsal surface. The halteres have dark brown to black stems and cream knobs.

Legs (Text-figs. 4 and 5): The legs are mainly dark brown to black, but in all legs the tibiae are light brown basally and the first hind tarsi have a very broad, light brown, median band, leaving only narrow apical and basal dark brown bands.

Most of the hairs on the legs are short and dark brown, but on the outer surface of the hind tibia there is a basal zone of dense light (usually golden) hairs. In addition, numerous spindle-shaped striated scales (Text-fig. 7) are to be found on the
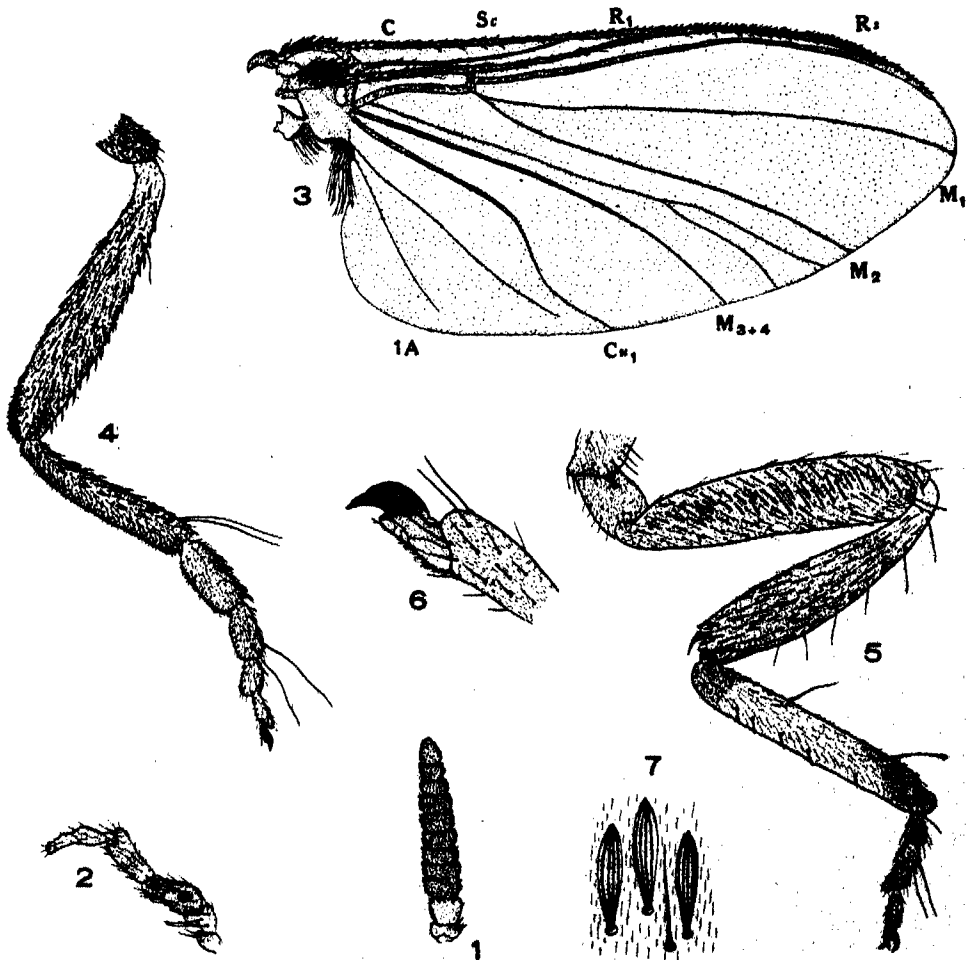
Text-figs. 1-7.—*Simulium papuensis*, n. sp. Female. 1, Antenna, × 300. 2, Palpus, × 300. 3, Wing, × 45. 4, Foreleg, × 70. 5, Hindleg, × 70. 6, Tarsal claws of hind leg, × 300. 7, Striated scales on femora and tibiae, × 300.

femora, tibiae and sometimes on the first tarsi. Finally, on the fore and hind tarsi there are a number of extremely elongated hairs—an apical pair on the anterior surface of the first and third fore tarsi, a single hair towards the apex of the first hind tarsus and a pair towards the apex of the third hind tarsal segments, the hairs on the hind tarsi not as long as those on the fore tarsi.

The hind tibiae are slightly angulated and a pair of stout spurs are present at the apex of all tibiae. In the hind leg the calcipalus (Text-fig. 5) is well developed, about three-quarters of the width of the first hind tarsus, but wider than the second. The pedisulcus is also pronounced.* The tarsal claws bear a small basal tooth (Text-fig. 6).

The relative lengths of the legs and leg segments are shown in the following table:

	Fore-leg, mm.	Mid-leg, mm.	Hind-leg, mm.
Total length	2·02	1·83	2·30
Coxa	0·25	0·23	0·27
Trochanter	0·14	0·16	0·16
Femur	0·45	0·47	0·57
Tibia	0·50	0·45	0·54
Tarsus I	0·32	0·25	0·50
Tarsus II	0·14	0·09	0·08
Tarsus III	0·10	0·06	0·06
Tarsus IV	0·05	0·05	0·05
Tarsus V	0·07	0·07	0·07

Thus the hind tibia is slightly shorter than the femur but a little longer than the corresponding first tarsal segment.

Wings (Text-fig. 3): At the base of the wing the veins are rather dark, the membrane slightly clouded, and the small basal cell† is absent. Macrotrichia are present on the upper surface of the basal section of the radius, continued along R_1, but here, in addition, there are a number of peg-like setae, similar to those found on the costa. Macrotrichia are absent on the upper surface of R_s except at the junction with the costa, but present on the undersurface of R_s. M_{3+4}‡ is sinuous.

Abdomen: The most striking features are the dense silver scales on the posterior margin of the first tergite and the complete covering of similar scales on the second tergite. The remaining tergites have silver scales over a dense black pubescence. From an obstructed view of the ventral surface it appears likely that there again the black pubescence predominates with scattered silver scales present, particularly abundant on the sides of the second and third segments. The colour of the scales on the abdomen changes with the direction and intensity of the light and they may appear light golden.

Male. Length 1·8-2·1 mm. Wing 2 mm.

Head: The clypeus is dull black with scattered silver-grey pubescence, the antennae and palpi are as in the female. The upper facets of the eye are extremely large, as large as the antennal sclerite, and with a diameter greater than that of the basal antennal segments (Text-fig. 8). Between the eyes there is a row of fairly strong hairs. The bucco-pharyngeal armature is as figured (Text-fig. 9).

---

* The calcipalus is an apical extension on the inner side of the first hind tarsus, and the pedisulcus a notch on the dorsal side of the second hind tarsal segment.

† In certain *Simuliid* genera, e.g., *Prosimulium* and *Cnephia*, a distinct small cell is present at the base of M, M_{3+4} and Cu_1.

‡ Following the notation used for the Nematocera by Tillyard (1927), but equivalent to Cu_1 of Smart, Edwards and others.

BB

Thorax: The arrangement of the scales, hairs and bristles on the mesonotum, scutellum and pleurae are as in the female, but the upper mesepimeral bristles appear more golden and are never completely dark.

The wings and halteres are similar to those of the female.

Legs: The main point of difference between the male and female legs lies in the much more angular hind tibia (Text-fig. 10) of the male. The fore tibia is again slightly longer than its corresponding femur and the tarsal claws bear a basal tooth.
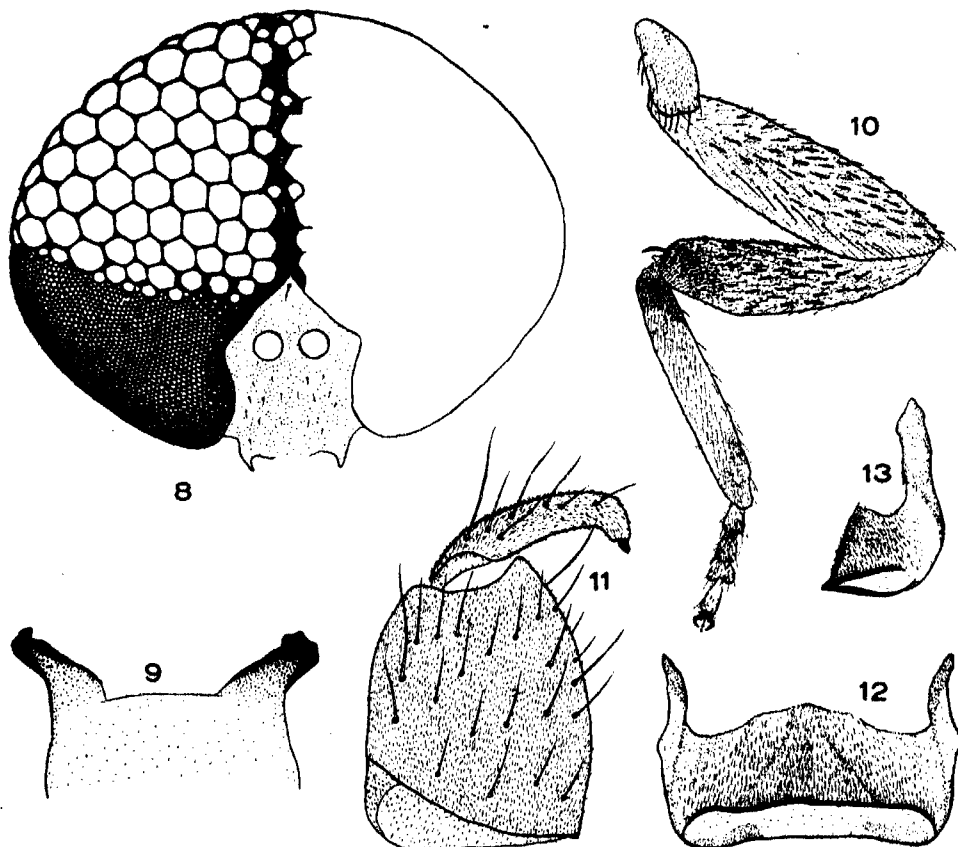
Text-figs. 8-13.—*Simulium papuensis*, n. sp. Male. 8, Head, dorsal view, × 60. 9, Bucco-pharyngeal armature, × 300. 10, Hindleg, × 70. 11-13, Genitalia, × 300. 11, Coxite and style. 12, Ventral plate, ventral view. 13, Ventral plate, lateral view.

Abdomen: The dense scales on the first two abdominal tergites and the scattered similar scales over a dense black pubescence on the remaining tergites are more golden than in the female.

Genitalia: (Text-figs. 11, 12 and 13.) The style (clasper) is shorter than the coxite (sidepiece), about five times as long as broad and bearing a single short spine at the tip. The ventral plate (aedeagus, adminiculum) appears to be simple, with well-developed basal arms.

Pupa. Length about 3 mm., light brown in colour.

On each side of the mid-line of the thoracic notum there is a longitudinal line of three (in one specimen, two) fairly stout hairs, and behind the base of the pupal gills there are two hairs on each side, again arranged longitudinally. The respiratory organs (pupal horns) are composed of some thirty to forty rather rigid, fine filaments arising from five or six main trunks (Text-fig. 14). These main trunks are about equal

In size, each trunk branching several times, the whole organ having a shrub-like appearance.

On the abdomen there are a number of spines carried on the apical margins of the segments, both on the dorsal and ventral surface. On each side of the mid-dorsal line (Text-fig. 15) there is a row of four short, stout spines on the third and fourth segments and a row of 8–10 much finer spines on the sixth, seventh and eighth segments (these spines are carried on small chitinized plates and may appear to arise at the base of the segments). Ventrally (Text-fig. 16), on each side of the mid-line, there is a pair of unequal fine spines on the fourth segment, a pair of larger bifid spines on the fifth segment (in both the fourth and fifth segments the spines closely approximated and submedian in position), and two bifid, widely separated spines on the sixth and seventh segments. The terminal segment carries a pair of upwardly directed stout spines.
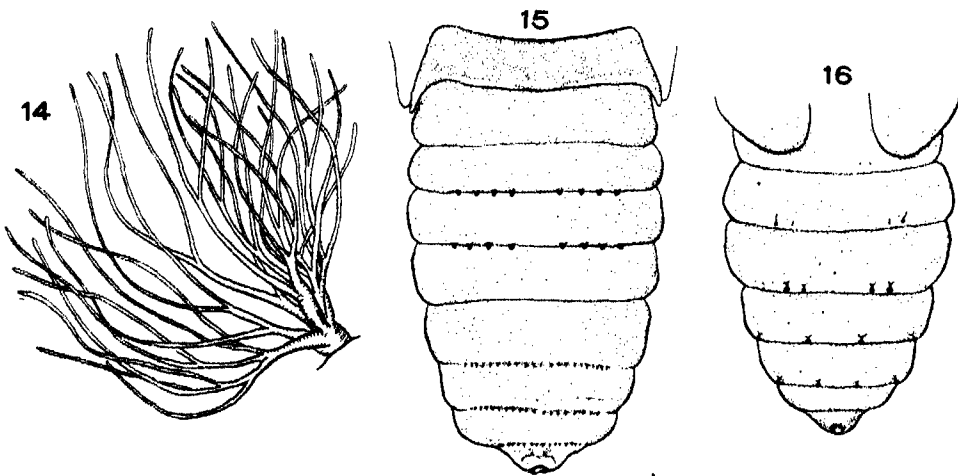
Text-figs. 14-16.—*Simulium papuensis*, n. sp. Pupa. 14, Respiratory organ, × 45. 15, Abdomen, dorsal view, × 45. 16, Abdomen, ventral view, × 45.

Cocoon.

Unfortunately the cocoons are not in good condition but appear to have a definite outline, with a complete flattened ventral surface which is applied to the support. There is a wide opening anteriorly, through which the anterior portion of the pupa, up to the base of the respiratory organs, protrudes. The texture of the cocoon is rather coarse, the individual threads being clearly visible.

Larva. Length 4·5 mm. General colour, grey.

Head: (Text-fig. 17.) The frontoclypeus is distinctly marked with a broad dark longitudinal band extending from the posterior margin of the head to beyond the level of the bases of the antennae. Along the mid-line two lighter spots are present on the band, the remainder of the head capsule showing pigmentation areas as illustrated (Text-figs. 17 and 21). The antennae, which are approximately equal in length to the base of the feeding-brushes, are composed of four segments, the joint between the first and second segments not complete. The first segment of the antenna is four-fifths of the length of the second, which is slightly shorter than the third segment (Text-fig. 18). The feeding-brushes bear about thirty-five long bristles, which carry subsidiary minute hairs on the distal half. The mandible (Text-fig. 19) has one large and two shorter strongly chitinized teeth and a small, blunt, strongly chitinized projection on its outer surface. From the concave surface of the large tooth protrude two fairly large and eight subsidiary teeth which are lightly chitinized. Finally, below these, there is a single weakly chitinized bifid tooth. The mentum

(Text-fig. 20) has a terminal row of nine teeth, the central and outermost tooth on each side (which bears a lateral projection) being the largest. Behind these, on each side, there are two teeth, also strongly chitinized, followed by three weakly chitinized teeth and an oblique row of five stout bristles. Towards the posterior margin, in the submedian area, there is a smaller bristle on each side.
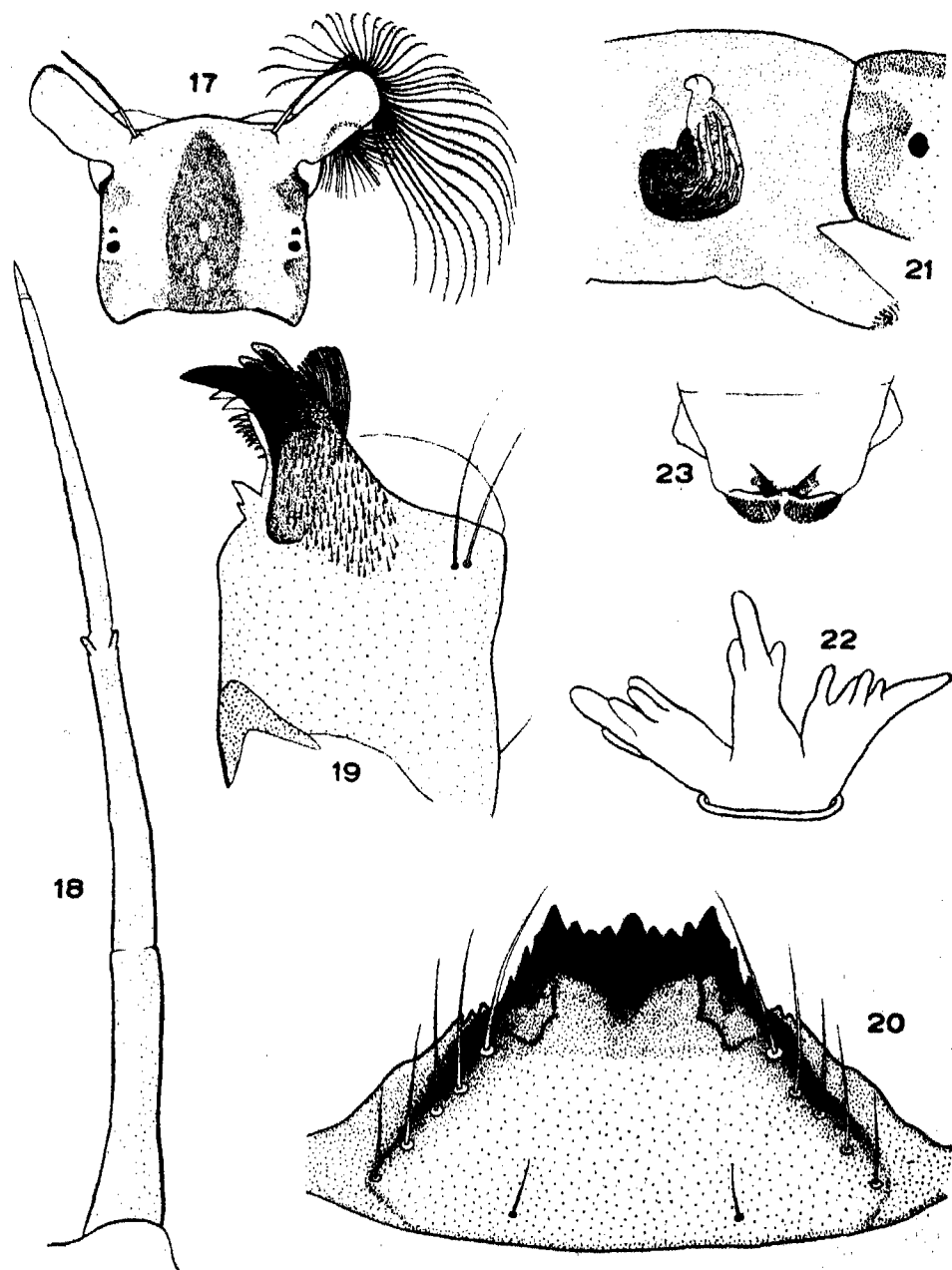
Text-figs. 17-23.—*Simulium papuensis*, n. sp. Larva. 17, Head, dorsal view, × 35. 18, Antenna, × 300. 19, Mandible, × 300. 20, Labium, × 300. 21, Pupal gill spot, × 45. 22, Anal gills, × 70. 23, Anal armature, × 45.

Thorax: The pigmentation of the thorax varies, but is always better developed on the ventral than on the dorsal surface. The gill spots (Text-fig. 21) of mature larvae are fairly large, almost triangular in outline.

Abdomen: A pair of basal tubercles are present on the ventral surface of the last abdominal segment. The anal gills (Text-fig. 22) are trilobed, the outer lobes with five to nine and the middle with three to five finger-like processes. The anal circlet is composed of some eighty to one hundred rows of hooks, each row with thirteen or fourteen stout bifid hooks. Anal armature as illustrated (Text-fig. 23).
Biology.

The larvae and pupae were collected on the undersurface of stones in a small, fairly rapidly running stream about thirty feet above sea-level. Together with *S. papuensis* were found the larvae and pupae of *S. ornatipes* Skuse.

Distribution: Port Moresby and Milne Bay,* New Guinea.

DISCUSSION.

The group to which I have ascribed *S. papuensis* has not as yet been defined by M. J. and I. M. Mackerras, who will do so in the near future when publishing the results of their discoveries in Queensland. These include the finding of two new species, closely allied to *S. papuensis* and to *S. faheyi* Taylor (1927), a species described from material collected in North Queensland. Although Enderlein's description of *S. wilhelmlandae* and *S. oculata* are quite inadequate, it is apparent that they closely resemble *S. papuensis*, and it is suggested that they also may belong to the group.

The pupa of *S. papuensis* is the first species in the genus *Simulium* to be recorded as having dendroid respiratory organs, which have hitherto been used as a generic character, typical only of the genera *Prosimulium* Roubaud and *Cnephia* Enderlein. With the exception of the pupal respiratory organs, *S. papuensis* is a typical *Simulium*.

KEY TO NEW GUINEA SPECIES OF SIMULIUM.
Males and Females.

Although it is not possible to formulate a simple, sound key to the New Guinea species an attempt is made below to tabulate the most obvious characters differentiating the species.

1. Femora with extensive yellow markings, tibiae with median yellow markings ....
   .... *S. ornatipes* Skuse
   Femora completely dark and only the bases of the tibiae with yellowish markings 2
2. Claws of male and female with a small basal tooth; first two abdominal tergites with dense
   silver scales, (antennae with basal segments light brown, remainder dark brown; hind
   tibia of male distinctly angulated, female hind tibia slightly angulated; first hind tarsus
   with broad median pale band) .... *S. papuensis*, n. sp.
   Claws of male simple; first two abdominal tergites bright yellow ochre (female unknown,
   antennae bright brown yellow; hind tibia angulated; first hind tarsus except for apical
   third bright yellow ochre) .... *S. wilhelmlandae* Smart
   Claws of male and female simple; abdomen dull brown, the last three tergites black and
   rather smooth, pubescence yellowish (colour of antennae, shape of hind tibia and
   colour of first hind tarsus not stated) .... *S. oculata* Enderlein

Note: Two females, collected by I. M. Mackerras at Milne Bay, New Guinea, in February, 1943, have been examined and show no significant morphological differences from *S. papuensis* apart from being larger (length 3·5 mm., wing 2·4 mm., foreleg 2·5 mm., midleg 2·3 mm., and hindleg 2·8 mm). It is possible that the immature stages or males may show differences, but until such time as the life history is known these specimens may be considered as *S. papuensis*.

REFERENCES.

DAVIS, CONNETT. and LEE, D. J., 1944.—The Type Concept in Taxonomy. *Aust. J. of Science,* 7 : 16-19.

EDWARDS, F. W., 1931.—Diptera of Patagonia and South Chile, Part ii. Brit. Mus. (Nat. Hist.), Lond., 121-154.

GIBBINS, E. G., 1936.—Uganda Simuliidae. *Trans. R. ent. Soc. Lond.,* 85 : 217-242.

LANE, J., and VULCANO, M. A., 1943.—A armadura bucal dos Simuliideos a seu valor taxonômico (Diptera, Simuliidae). *Rev. de Entomologia,* 14 : 430-440.

DE MEILLON, B., 1930.—On the Ethiopian Simuliidae. *Bull. ent. Res.,* 21 : 185-200.

TAYLOR, F. H., 1927.—Two new species of Australian Culicidae (Diptera) and a note on *Simulium bancrofti,* Taylor, with the description of a new species of *Simulium* (Dipt.). *Bull. ent. Res.,* 18 : 67-72.

WAHLENBERGIA LIMENOPHYLAX.

By N. LOTHIAN,
Botanical Gardens, Adelaide, South Australia.

In my paper on the Australasian species of *Wahlenbergia,* published in the PROCEEDINGS OF THE LINNEAN SOCIETY OF NEW SOUTH WALES, vol. lxxi, 1946, 233, the above species unfortunately appeared under the name *W. limnophalyx.* This was an unintentional orthographic error, for which I alone am responsible, and was due to my inability to consult certain notes and the type material at the time of final checking.

The correct name of the species is *Wahlenbergia limenophylax* Lothian, with which name the type material has been inscribed. I trust that this alteration will be accepted under Article 70 of the International Rules of Botanical Nomenclature (1935).

The natural habitat of this species is on the tops of sea cliffs and adjoining areas at Lord Howe Island. Such cliffs overlook the harbour. The specific epithet in its correct form means a harbour watcher, and refers to this habitat. The epithet "limnophalyx" would give one the impression that the plant inhabits swamps or marshes, and would be quite misleading, so that correction of my mistake appeared necessary.

STUDIES IN THE METABOLISM OF NORMAL AND REGENERATING TISSUE OF THE EARTHWORM.

PART 1. FACTORS AFFECTING THE ENDOGENOUS OXYGEN CONSUMPTION OF NORMAL AND REGENERATING MUSCLE TISSUE.

By B. R. A. O'BRIEN, Department of Anatomy, University of Sydney.

(Eight Text-figures.)

[Read 24th September, 1947.]

INTRODUCTION.

The purpose of this investigation was to establish certain information related to the techniques used for the examination of respiratory mechanisms, functioning throughout the processes of tissue repair and reorganization. Experimental work on the respiratory activity of annelid tissue has been in most cases to develop the concept of Metabolic Gradient elaborated by Child and his school.

Respiratory activity as a function of segmental level has been investigated in several of the Polychaetes and Oligochaetes. Hyman and Galegher (1921) obtained a U-shaped curve describing the antero-posterior gradient for oxygen consumption (Qo_2), in two forms of *Nereis* and one species of *Lumbriculus*, the estimation of oxygen being carried out according to the Winkler method. Shearer (1924) demonstrated that the anterior Qo_2 was approximately twice that of the posterior, using both small pieces of worm and acetone powders. Perkins (1929) confirmed the result obtained by Hyman and Galegher, in that he obtained a similar gradient curve for Qo_2 in *Lumbricus* and *Allolobophora*. In an effort to ascertain whether a relation existed between "growth" metabolism and this gradient he estimated the total iodine equivalence, –SH, and total S, but found no correspondence with the observed Qo_2 data. Okada (1929) and Kawaguti (1934) obtained a U-shaped curve for both Qo_2 and Qco_2 in an Oligochaete Branchiura.

Maloeuf (1935), using very small pieces of worm in order to eliminate motor activity, concluded that no significant difference occurred in the Qo_2 at different levels of the earthworm, and that the effect obtained by other workers was due to motor activity in the pieces examined.

In general the work done on the respiratory activity among the Annelida appears to demonstrate that a gradient in Qo_2 exists. Little work has been carried out either utilizing manometric techniques or from the viewpoint of the relative response of metabolic systems to the growth and organization requirements imposed upon the organism following injury. Hyman (1932), using the Winkler technique, examined the Qo_2 of *Nereis virens* after injury and in the case of posterior tissue obtained a depression in Qo_2 relative to the normal tissue and concluded that posterior tissue following injury exhibits a subnormal Qo_2. With reference to the development of this project it was necessary to consider the possible sources of variation which may arise both within the tissue of the organism and in the methods of investigation when comparisons are made between experiments differing in design. The following report has been confined to the determination of such conditions as appear optimal for the survival and metabolism of the tissue during experimental treatment, and to the investigation of the endogenous oxygen consumption of early regeneration tissue.

Material.

The organism concerned was a species of earthworm, belonging to the genus *Allolobophora*. The population from which samples were taken was obtained from garden soil at Mosman, Sydney. The culture was maintained in glass troughs filled

with damp earth. The worms were fed on crumbed bread and periodically the earth
was replaced.

The tissue used was the muscular layer, consisting essentially of circular and
longitudinal muscle bounded externally by a thin cuticular layer.

Methods and Results.

(i) *Selection of experimental lots. Specimens for experimentation were selected
in the following manner*: The worms when first obtained were segregated into four size
classes, A+, A, B, and C, defined within certain limits of the total length, and the diameter
of the post-clitellum region. These limits are indicated in Table 1.

TABLE 1.

Class.	Total Length (cm.).	Diam. (cm.).
A+	> 14	> 0·4
A	11–14	0·3–0·4
B	7–10	0·2–0·25
C	5–7	0·1–0·2

These dimensions obtained from anaesthetized, relaxed specimens form classes into
which worms may be placed at sight with little difficulty.

Material for experiments was then selected without bias from the respective classes
consisting mainly of 50 worms, which in turn was selected from a population of 200 or
250 per group, there being one or more of the latter groups per size class, depending
upon the number of worms in the entire culture.

(ii) *Preparation of tissue.*—The portion of the worm required was cut off, split
longitudinally, and the viscera, including the nerve cords, carefully scraped away from
the muscle. The muscle strip was then washed rapidly in two changes of distilled water,
dried carefully on filter paper and placed on a glass slide over ice. When sufficient
tissue had been prepared the strips were transferred to a clean dissecting board, cut
into squares approximately equal in area, thoroughly mixed and transferred as
equivalent portions to glass slides of known weight. The slide plus tissue was weighed
and the latter transferred to the Warburg vessels, the medium in which was ice-cold. Thus
the mixed tissue mass from which that required for each experimental unit was obtained,
was composed of tissue from several worms, the number dependent on experimental
requirements. A variation may arise because of the selection of different numbers in
certain experiments. In view of this the relationship between the number selected
from a lot and the consistency of the result obtained was examined within the limits of
the work concerned. Table 2 indicates that the variation between lot 1, 2, 3, of Set I

TABLE 2.

Set.	Lot.	No./Lot.	No. Selected.	Wt. of Tissue.	ul. O_2/60 min.
I	1	50	10	100 mg.	14·1
	2	50	20	100 mg.	13·8
	3	50	50	100 mg.	14·2
II	1	50	10	200 mg.	30·2
	2	50	20	200 mg.	30·8
	3	50	50	200 mg.	31·8
III	1	50	20	100 mg.	14·6
	2	50	20	100 mg.	14·1
	3	50	20	100 mg.	14·8

and Set II is no greater than that between three lots of the same number, Set III. Throughout the work the procedure followed has been a selection of 20 worms per lot of 50.

(iii) *Measurement of* Qo_2.—The oxygen consumption was measured by the standard Warburg technique (Warburg, Dixon, Umbrelt), the tissue squares being suspended in 3 c.c. of an aqueous salt solution. The CO_2 was absorbed by 20% KOH and paper. The manometers were shaken at approximately 90 oscillations per minute in a bath at a temperature of 27°C.

(iv) *Medium*.—The following media for the suspension of the tissue were investigated:

Medium.	NaCl (gm.).	KCl (gm.).	$MgSO_4 7H_2O$.	$CaCl_2$ (gm.).	$(PO_4.)$	H_2O (c.c.).
Ringer	0·864	0·023	0·038	...	—	100
Ringer–PO_4	0·864	0·023	0·038	—	...	100
Amphibian Ringer–PO_4 ..	0·650	0·014	—	0·012	—	100
Krebs–Henslelt	0·900	0·046	0·037	0·038	—	100
Krebs–Henslelt–PO_4	0·900	0·046	0·037	0·038	—	100
M/100 PO_4—buffer distilled water	0·5 ml. of M/15 PO_4 buffer per 3 ml. H_2O					

The media containing phosphate are made up by adding 0·5 ml. of M/15 PO_4-buffer to the medium concerned in the respirometer flask. The pH of the media was adjusted to 7·5 by addition of N/10 NaOH where required.

The investigation is recorded in Table 3 and shows little difference between the three Ringer solutions and the PO_4-buffer solution, whereas both the Krebs-Henslelt solutions and the distilled water alone, gave low values for the Qo_2. Throughout the following work Amphibian-Ringer-PO_4 was the medium selected, this being similar in freezing point depression to earthworm blood, which has a value −0·45 to −0·51 (Hellbrunn).

TABLE 3.

Medium.	pH.	Wet Wt. Tissue.	Temp. °C.	ul O_2/hr.
Ringer	7·5	200 mg.	35° C	44·7
Ringer–PO_4	,,	,,	,,	43·1
Amphibian–Ringer–PO_4	,,	,,	,,	46·5
Krebs–Henslelt	,,	,,	,,	30·6
Krebs–Henslelt–PO_4	,,	,,	,,	27·6
PO_4 buffer (M/100)	,,	,,	,,	42·2
Distilled water	,,	,,	,,	28·4

(v) *Tissue mass.—Fluid volume variation*: The amount of tissue per flask was selected with two ends in view—namely, to yield an easily measurable oxygen uptake and to conserve tissue. In general approximately 100 mgs. wet weight was considered sufficient. Table 4 indicates the Qo_2 for different weights of tissue. In all cases the volume of the medium was 3·0 mil. per flask, consequently by varying the amount of tissue the tissue/volume ratio is changed. The effect of an increase in the value of this factor is apparent from both Tables 4 and 5, where the departure from a linear relationship between tissue weight and Qo_2 is marked.

TABLE 4.
Temp. 37° C.   pH 7·5.

Wet Wt. Tissue.	30 Min.	60 Min.	90 Min.
50 mg.	3·7 ul.	10·9 ul.	16·5 ul.
100 mg.	13·4 ,,	24·4 ,,	34·5 ,,
200 mg.	34·0 ,,	56·1 ,,	88·5 ,,
400 mg.	74·4 ,,	134·5 ,,	190·0 ,,

Table 5 expresses the Qo_2 over a period of 120 minutes for three tissue/volume ratios, of 0·18, 0·08 and 0·06, relative to three positions along the worm, viz., (1) the terminal posterior 10 segments, (2) the 11th–20th, and (3) 21st–40th.

TABLE 5.
Temp. 27° C.   pH. 7·5.

Wt. tissue (wet) mg.	550			250			180		
Tissue/ vol. ratio	0·183 ≑ 0·2			0·083 ≑ 0·1			0·060 ≑ 0·05		
Time (min.)	0–10 (A₁)	10–20 (A₂)	21–40 (A₃)	0–10 (B₁)	11–20 (B₂)	21–40 (B₃)	0–10 (C₁)	11–20 (C₂)	21–40 (C₃)
35 min.	80·5 ul.	74·6 ul.	55·5 ul.	37·4 ul.	28·0 ul.	17·1 ul.	17·4 ul.	17·0 ul.	16·2 ul.
60 min.	128·5	119·5	92·0	64·2	40·5	42·0	33·0	34·2	30·8
120 min.	238·5	216·3	168·0	114·0	84·1	73·0	57·3	56·3	53·5

In order to minimize the variation between experiments where the tissue/volume ratio differs the extent of this error should be ascertained and the experimental results adjusted before comparison is made. Fig. 1 shows the Qo_2 of Table 5 plotted as a function of time, the Qo_2 expressed as ul of O_2/100 mg. wet weight tissue. It can be readily seen that as the ratio increases beyond 0·05 the error introduced by reducing results to ul/100 mg. tissue becomes considerable.

(vi) *Limiting thickness of tissue.*—The importance of this source of error has been stressed by those workers concerned with tissue slice experiments; an additional factor may be introduced by this tissue, namely, its increase in thickness due to a contraction effect during the experiment. Both the limiting thickness and the increase due to contraction have been investigated. Squares of tissue, prepared as described, were dried carefully, weighed, and the surface area measured, from which values an approximate measure of thickness was obtained, assuming the tissue density to be unity. Table 6 gives the result for the average thickness of mixed slices from worms belonging to classes A⁺, A, and B.

TABLE 6.

Size Class.	No. Samples.	Mean Thickness.
A	100	0·5 mm.
A	,,	0·35 mm.
B	,,	0·22 mm.
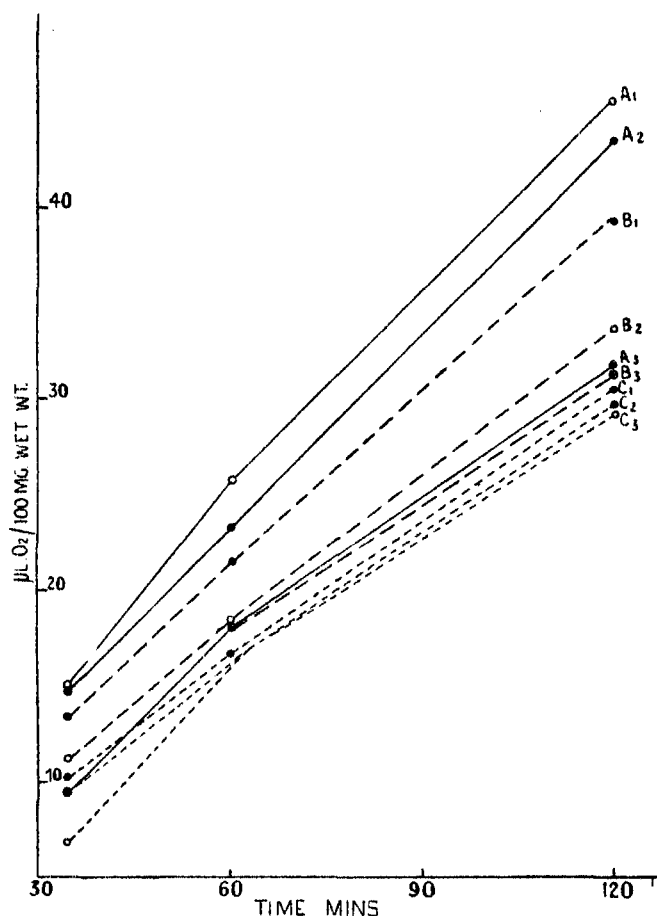
Fig. 1.—Relation between Q_{O_2} expressed as ul of $O_2/100$ mg. wet wt. of tissue, and time.

Table 7 shows that a small increase in thickness occurs after the tissues have been shaken in a flask for 30 minutes. This increase may be due to a contraction effect produced by the medium.

TABLE 7.

Size Class.	Sample No.	Av. Initial Thickness.	Av. Final Thickness.	Percentage Increase.
A	100	0·31 mm.	0·34 mm.	12

These results were then examined according to the formula devised by Warburg, which is claimed to yield a reliable estimate of the limiting thickness for O_2 consumption in a given tissue. The limiting thickness d' is given by:

$$d' = \sqrt{8 \; Co \; \frac{D}{A}}$$

where   Co = Concentration of O_2 outside tissue.
D = Diffusion const. for O_2 in ml. at N.T.P.
Krogh's value for tissue at 38°C. = 1·4 × 10⁻⁸
A = O_2 consumption of tissue per unit volume and time.

Table 8 shows the values of d' calculated from data obtained from Tables 4 and 6.

TABLE 8.

Class.	Mass Tissue (gm.).	Vol. Tissue (c.c.).	Time Min.	Mls. of O_2.	d'.
A	0·100	0·1	60	$24·4 \times 10^{-8}$	0·7 mm.
A	0·200	0·2	90	$88·5 \times 10^{-8}$	0·6 mm.
A	0·050	0·05	60	$10·9 \times 10^{-9}$	0·7 mm.

If 0·6 mm. is taken to be the limiting value then the tissue used throughout should not be subject to diffusion limitations. Tissue from worms of class A⁴ was considered unacceptable since when the 12% contraction effect is added it tends to approach the limiting value when the possible error of this factor is also considered.

(vii) *Oxygen Pressure.*—The effect of an increase in oxygen concentration was examined in order to provide an additional check on the question of limiting thickness. Gas mixtures containing 20%, 70%, and 100% oxygen were made up from commercial cylinders of air and pure oxygen. The results are indicated in Table 9.

TABLE 9.

Size Class.	Experiment.	ul O_2/100 mg. wet wt./hr.		
		20% O_2.	70% O_2.	100% O_2.
B	I	16·3	16·9	12·6
B	II	17·1	——	15·7
B	III	15·9	15·7	13·6

This additional evidence suggests that no limitation due to diffusion of oxygen resulted from the tissue thickness used. The depression in Qo_2 observed in pure oxygen does not concern this report and will be covered in greater detail in further work. It was considered that any difference between the 20% and 70% values was not significant and that the gas phase could safely be air.

(viii) *Area of tissue squares.*—The question of the relationship between the oxygen consumed and area of tissue square was examined. Class B worms were used and squares prepared of three surface area values. Table 10 indicates that a slight inverse relation may exist between these factors. This appears to be to some extent a function of area *per se* as indicated by a diminution in the effect at a higher oxygen tension; however, an additional factor due to increase in tissue damage where the smaller squares are concerned may also be important.

TABLE 10.

Size Class.	Mean Area (mm.²).	ul O_2/Mg. total N/hour.		
		20% O_2.	70% O_2.	100% O_2.
B	18·3	11·6	17·5	12·2
	9·7	——	14·7	14·5
	4·3	17·8	18·1	17·9

In view of the difficulties involved in estimating an effect due to tissue damage in any quantitative manner it was the practice throughout to perform all experiments at a constant "tissue area" value. The value selected was that approximating 4·3 mm.² and the error involved in preparation was of the order ± 1 mm.². Thus if comparative experiments are run with similar tissue mass and similar area of tissue squares the possibility of errors due to a function of area and tissue damage are minimized.

(ix) *Size of worm in relation to* Qo_2.—Worms of the three size classes, A, B, and C, were taken and two tissue regions prepared from each specimen. (i) Tissue from the 15 posterior terminal segments and (ii) tissue from the 15th–40th posterior segments. Fig. 2 indicates a variation between the groups concerned; however, it is considered that, although the difference between the A-worms and the two smaller may be significant, that between B- and C-worms is not significant, being due to experimental error. Throughout this work worms of size class B have been used unless otherwise stated.

(x) *Segmental level in relation to* Qo_2.—A variation in Qo_2 was found to exist between the terminal posterior segments and those anterior to them. It was considered necessary to investigate the extent of this variation in relation to segmental level, with the aim to select some portion of the posterior tissue which showed a relatively constant Qo_2. Posterior tissue was prepared from a lot of 50 worms and divided into the following categories:

(a) Terminal 10 segments.
(b) 11th to 20th segments.
(c) 21st to 35th segments.
(d) 35th to 55th segments.
(e) 55th to 70th segments.

The results are indicated in Table 11 and Fig. 3.

TABLE 11.

Exp.	Qo_2 as µl O_2/100 mg. wet weight.				
	0–10 (a)	11–20 (b)	21–35 (c)	35–55 (d)	55–70 (e)
I	16·7	12·0	—	—	11·6
II	17·5	11·8	12·1	13·0	10·0
III	17·4	12·1	11·9	12·4	12·6
Mean	17·2	11·9	12·0	12·7	11·4

A higher Qo_2 value is observed in the terminal group of segments than in those anterior to them up to the level of the 70th segment, and the respiratory activity appears to show little variation between the 10th and 70th segment. This result is also indicated in Fig. 2, where the terminal group of 15 segments exhibits a higher Qo_2 than the group 15th–40th. In order to ensure a comparatively stable rate of oxygen consumption tissue for examination was taken from the 20th to the 40th segmental level unless otherwise stated.

(xi) *pH effect*.—The Qo_2 was investigated over a range of pH values from 5·8 to 8·6. The medium used was Amphibian Ringer made up in M/100 PO₄-buffer at the pH required, N/10 NaOH was added to obtain the 8·6 value. The pH was checked at the conclusion of each experiment with a glass electrode. No alteration was found to have occurred. Fig. 4 shows the Qo_2 obtained plotted as a function of pH, and indicates the presence of a plateau between 7·4 and 8·2 at 27°C., whereas Fig. 5 shows the optimum shifted to a lower value as the temperature increased. These results indicated that the pH should be maintained at 7·4 to 7·5 throughout the work.

(xii) *Temperature effect.*—Experiments were carried out over a range from 16°C. to 40°C., the duration of an experiment being 90 minutes. At 40°C. no drop in the respiratory rate had occurred. Fig. 6 summarizes these observations. The effect on Qo_2 over the above range in relation to previous environmental temperatures was examined. Worms were kept at room temperature (20°C.–23°C.), at 25°C. and at 28°C. No variation in results was noticed, so that any error arising from the fact that the organisms were not maintained in an environment of constant temperature was negligible; however, in the experiments to follow dealing with the regenerating tissue the worm population and the experimental lots were maintained at 27°C.
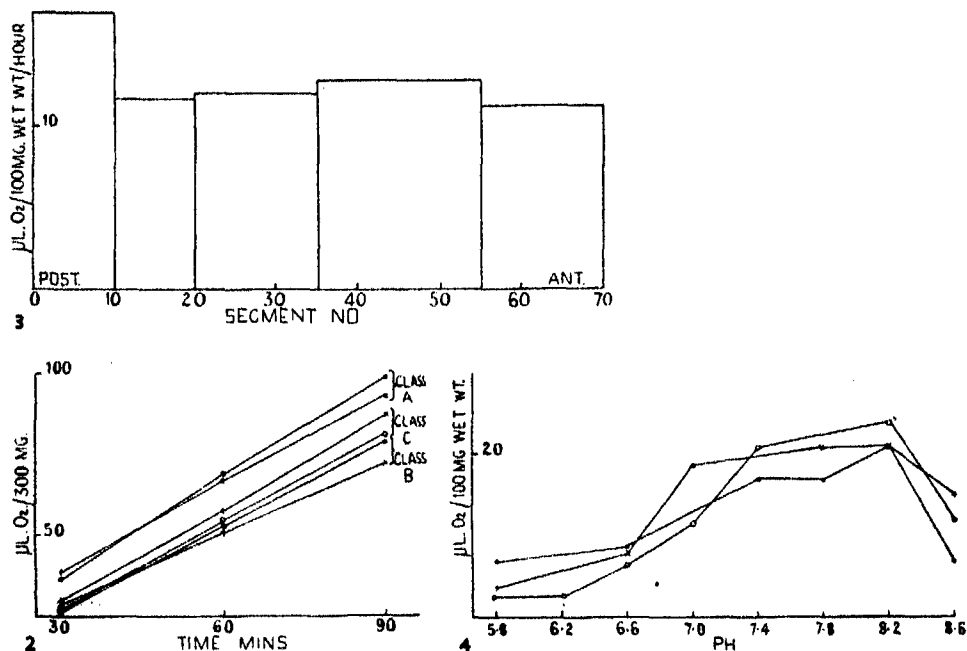
Fig. 2.—Qo_2 plotted against time for three size classes, A, B, C, and two tissue regions. O — terminal 15 segments + — 15th to 40th post. segments.

Fig. 3.—Histogram prepared from Table 11 relating Qo_2 and position of tissue (as segment No.) on the worm.

Fig. 4.—Qo_2 as ul. $O_2/100$ mg. wet wt. of tissue as a function of pH.

(xiii) *Expression of results.*—Results are expressed as ul of O_2 consumed by 100 mg. wet weight of tissue and in some cases the Qo_2 is related to total nitrogen. In consequence of this a number of estimations were carried out in which the relationship between Wet Weight, Dry Weight and Total N was ascertained. The relation between Wet Weight and Dry Weight may be expressed by the regression equation $y = 5 + 5\cdot1x$ where x and y are dry and wet weight respectively; and that between Dry Weight and Total Nitrogen by the equation $y = -0\cdot2 + 12\cdot5x$ where x represents Total Nitrogen.

(xiv) *Estimation of Total Nitrogen.*—Total Nitrogen was estimated in the following manner: At the conclusion of an experiment the KOH-paper was removed from the respirometer flask and any excess KOH neutralized by addition of a few drops of sulphuric acid (approximately 50%). The flask contents were then washed into a one-inch diameter boiling tube. The tubes were then placed upright in an oven and the contents evaporated to dryness; 0·5 ml. of 50% sulphuric acid, together with several drops of hydrogen peroxide, were then added and the contents digested over a small flame for 30 minutes. The digest was then washed into a 100 ml. volumetric flask made up to 100 ml. and set aside for analysis.

The analysis carried out was a typical Nesslerization followed by colorimetric comparison with a standard.

ENDOGENOUS OXYGEN CONSUMPTION FOLLOWING INJURY.

(i) *Qo_2 following injury at the 30th segmental level.*—Approximately 300 worms were selected; 150 were injured by cutting off the posterior 30 segments; 150 remained uninjured. Each lot was returned to a separate container filled with similar moist earth and maintained at 27°C. At periods of 24 hours, 72 hours, and 168 hours a sample of 30 specimens was taken at random from each lot and tissue prepared. The tissue of the regenerating portion consisted of the terminal 5 segments as less was difficult to prepare rapidly. Consequently as the worms regenerated a higher percentage of the tissue taken consisted of regenerate. At 24 hours about 10% wet weight was regenerate, at 48 hours about 30%, at 72 hours 50% and at 168 hours approximately 70–80%. These figures were obtained by previously examining regenerating worms and weighing the apparently new tissue formed, hence may involve considerable error as in the early stage much may be mucus or damaged tissue rather than new tissue and in the later stages a low estimate may occur following difficulty in distinguishing the regenerating tissue. However these estimates are given mainly as an indication of the relative amounts of tissue in the sample.

Two tissue portions were taken from the normal uninjured worms: (1) the terminal 10 segments and (2) the tissue from the 30th to 40th levels. The normal tissue was included so as to indicate possible change in Qo_2 following the injury and to enable comparison to be made between the two normal levels of oxygen uptake and that accompanying regenerative activity. The results obtained are given in Table 12, the Qo_2 expressed as ul of O_2 per mg. total nitrogen, and in Fig. 7, where Qo_2 is represented as a function of time.

TABLE 12.

Exp.	Time (min.).	24 Hrs.			48 Hrs.			72 Hrs.			168 Hrs.		
		R	N_1	N_2	R	N_1	N_2	R	N_1	N_2	R	N_1	N_2
I	15	1·1	1·3	2·1	0·9	0·9	---	0·8	1·0	1·9	2·3	1·0	2·1
	30	3·2	3·0	5·3	3·3	---	6·7	4·2	3·1	4·6	6·3	3·9	5·7
	60	7·0	7·4	14·0	8·2	8·5	12·9	10·1	7·1	13·1	11·4	8·3	12·6
II	15	1·0	---	---	0·8	1·0	2·2	---	---	---	2·4	0·8	2·0
	30	4·1	---	---	3·9	4·5	8·1	4·5	4·4	8·6	7·8	5·0	8·7
	60	7·5	---	---	9·2	7·6	13·7	11·2	10·0	14·3	13·2	8·2	14·8

R = Tissue from regenerating portion of injured earthworm.
N_1 = Tissue from 30th-40th segs. normal worm.
N_2 = Tissue from 0-10th segs. normal worm.

(ii) *Endogenous Qo_2 and effect of previous injury.*—With further work in view it was felt necessary to consider the possibility of variation arising as a function of previous, recent injury. The experiment was arranged so that two periods, 48 hours and 72 hours following injury, were studied. Each period contained the following groups:

(a) Worms regenerating at the 30th segmental level for first time.

(b) Worms regenerating at the 30th segmental level following a previous injury at that level 48 hours before section.

(c) Worms regenerating at the 30th segmental level following two previous injuries at that level 48 hours apart and 48 hours prior to section.

By the 30th segment is understood the original segmental level of the first injury.

The results are indicated in Table 13, and are referred to 100 mg. wet weight of tissue.

TABLE 13.

Time (min.).	48 Hrs. After Injury.			72 Hrs. After Injury.		
	No. of Previous Injuries.			No. of Previous Injuries.		
	0	1	2	0	1	2
15	1·1	1·0	—	1·1	—	1·4
30	5·4	3·2	4·1	5·9	5·9	5·7
60	12·8	11·7	11·9	14·1	13·4	14·3

(iii) *Endogenous Qo₂ in tissue adjacent to injury.*—Worms injured 72 hours previous to the experiment were used. Three portions of tissue were taken from the injured worms:

(*a*) Terminal regenerating portions to approximately the 5th segment.
(*b*) Adjacent tissue from 5th to 10th segment.
(*c*) Tissue from between 40th and 50th segments.

The results are expressed as ul of O_2 per 100 mg. wet weight and are tabulated in Table 14.

TABLE 14.

Worm Tissue.	Segments.	15 Min.	30 Min.	60 Min.
Injured	0–5	1·2	5·9	14·2
	6–10	1·6	3·2	9·5
	30–40	2·2	4·3	10·0
Uninjured	0–10	1·7	3·5	12·3
	30–40	2·3	—	9·7

Fig. 8 indicates the increase in Qo_2 occurring in both the terminal segments of the normal worm and in the regenerating portion of the injured, compared with the lower value for tissue adjacent to the injury which exhibits a similar activity to the 30th–40th level on the normal worm.

DISCUSSION OF RESULTS.

An attempt has been made to establish experimental procedure for the examination of this particular tissue in order to facilitate further work on this project. The experiments reported are rather to indicate possible sources of variation and the extent of the error involved when comparisons are to be made, than to present a detailed examination of the factors concerned *per se*.

The apparent gradual increase in the Qo_2 of the regenerating portion from the relatively low value typical of the 40th segmental level to the higher value exhibited by the normal terminal segments may be due either to a gradual increase in the metabolic rate of the tissue with time or to an increase in the percentage of tissue characterized by a higher Qo_2 in the sample. If a large proportion of the tissue obtained shows a low Qo_2 value relative to that exhibited by the actual regenerate then any increase due to regenerating tissue would be moderated if only a small proportion of the latter tissue was present. Table 14 and Fig. 8 suggest that the latter explanation
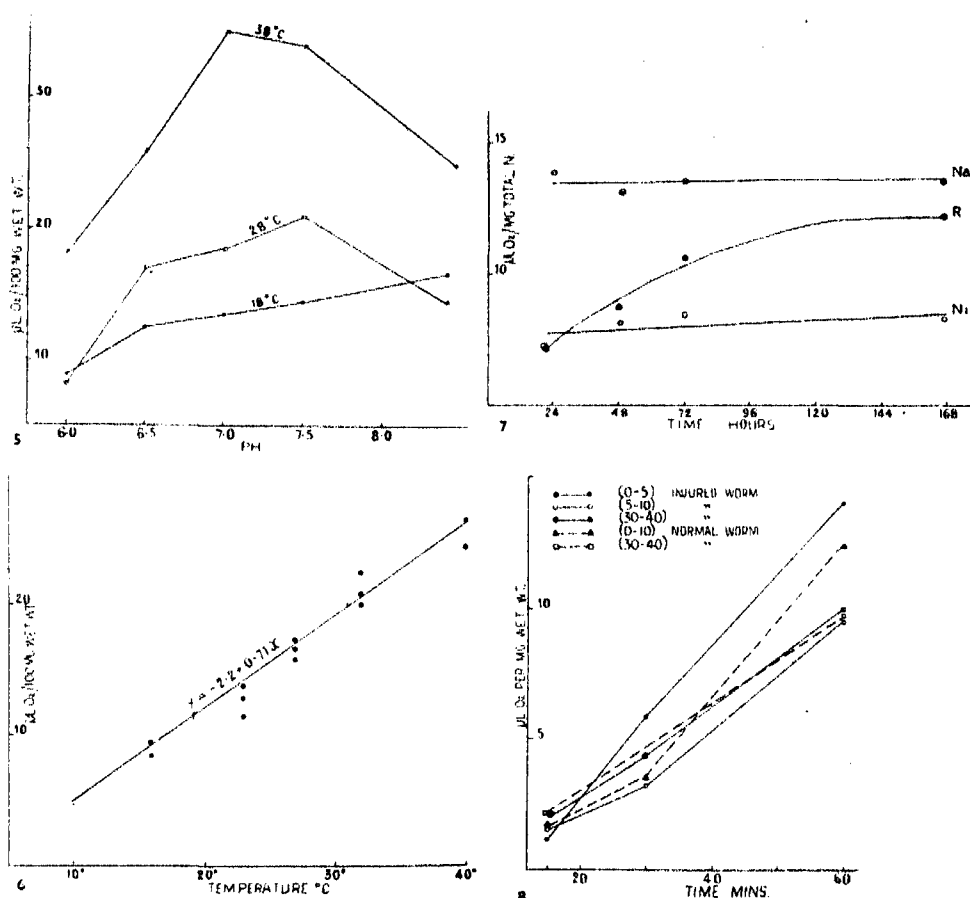
Fig. 5.—Qo_2 plotted as a function of pH at temperatures 18°C., 28°C., 38°C.

Fig. 6.—Qo_2 plotted as a function of temperature over a range from 16°C. to 40°C.

Fig. 7.—Showing the relationship between the respiratory activity of uninjured tissue at two levels. N_1 — level of 30th-40th seg., N_2 — terminal post. tissue and regenerating tissue at 30th segmental level. R. over a period of 168 hours.

Fig. 8.—Respiratory activity of uninjured tissue, regenerating tissue and tissue adjacent to injury.

is possible and that tissue at the 40th segmental level is transformed from one of a relatively low Qo_2 to one characteristic of terminal growing tissue. The question then to be considered is the rate at which this transformation takes place. Taking into account the approximate proportion of regenerate in the sample it would appear that little difference occurs during the first 30 hours but that after this period the apparent transformation time is increased·by the depressing effect of uninjured tissue present in the sample. When it is considered that the regenerating tissue is formed rapidly in response to injury and that organization and growth are superimposed upon the initial cellular mass, it is reasonable to expect an increase in metabolic activity and, provided that the metabolic pathways are predominantly aerobic, an increase in Qo_2 should occur. The question of the effect of previous injury is one which is being considered in more detail, especially in relation to food storage and starvation. Table 13 was included to show that in well fed worms recent injury was not an important source of variation within the limits of the experiment described.

The increase in oxygen consumption appears to be related to a large extent to an increase in total dehydrogenase and in particular to succinic dehydrogenase; however, this work is as yet incomplete and will be reported later.

SUMMARY OF RESULTS.

(i) The endogenous oxygen uptake exhibited by posterior muscle tissue in the earthworm *Allolobophora* sp. has been investigated.

(ii) Possible sources of variation due to experimental technique have been examined and an indication given of the optimal experimental conditions for this tissue.

(iii) The terminal posterior segments have been shown to maintain a higher Qo_2 than those anterior to them and that the Qo_2 of regenerating tissue at a level of low value increases towards the higher value as regeneration proceeds.

(iv) The effect of previous recent injury was found to be slight and of no great significance, relative to the work concerned.

ACKNOWLEDGEMENTS.

REFERENCES.

DIXON, M., 1943.—Manometric Methods. Cambridge.
HEILBRUNN, L. V., 1945.—General Physiology. (Saunders.)
HYMAN, L. H., and GALEGHER, A. E., 1921.—Direct Demonstration of a Metabolic Gradient in Annelids. *J. Exp. Zool.*, 34 : 1-16.
HYMAN, L. H., 1932.—The Axial Respiratory Gradient: Experimental and Critical. *Physiol. Zool.*, 5 : 566-592.
KAWAGUTI, S., 1932.—Studies on the Disintegration of Branchiura by Methylene Blue. *Mem. Fac. Sci., Taihoku Imp. Univ.*, 7 : 57-67.
MALOBUF, N. S. R., 1936.—Metabolic Gradient in the Adult Earthworm. *Biol. Zbl.*, 56 : 429-36.
OKADA, T., 1929.—Respiration of Branchiura. Abstracted from C. M. CHILD, Patterns and Problems of Development. 1941. Chicago.
PERKINS, M., 1929.—Growth Gradients and the Axial Relations of the Animal Body. *Nature*, 124 : 616.
SHEARER, C., 1924.—On the Oxygen Consumption Rate of Parts of Chick Embryo and of Segments of the Earthworm. *Proc. Roy. Soc. Lond.*, B, 96 : 146-156.
UMBREIT, W. W., BURRIS, R. H., STAUFFER, J. F., 1945.—Manometric Techniques and Related Methods for Study of Tissue Metabolism. (Burgess.)
WARBURG, O., 1930.—Metabolism of Tumours. (Constable.)

RESISTANCE TO BARLEY LEAF RUST (*PUCCINIA ANOMALA* ROST.).*

By I. A. WATSON and F. C. BUTLER.

[Read 24th September, 1947.]

INTRODUCTION.

Although considerable work has been done on the genetics of barley in the United States, little is known of the way in which resistance to leaf rust (*Puccinia anomala*) is inherited. Studies have been made of the reactions of barley varieties to this disease, but, as far as the writers are aware, it is not known whether an allelic series of genes controls the different types of resistance that have been found or whether several loci are involved. In this country the only reported work dealing with the genetics of resistance to barley leaf rust was done by Waterhouse (1927), and he found simple monofactorial segregations in crosses between resistant and susceptible types.

The disease is not of economic importance in New South Wales. It occurs commonly along the eastern coast but never reaches epiphytotic proportions in the main barley growing areas of the State. Hence this study was not connected with any breeding project but was undertaken to determine whether the occurrence of several factors for resistance to barley mildew, *Erysiphe graminis Hordei*, as found by Briggs and his colleagues in California, was paralleled by a similar group for resistance to *P. anomala*. This paper presents our preliminary results.

VARIETAL REACTIONS.

Throughout the work the same rust culture was used as that previously reported upon (Waterhouse, 1927). At the time when this latter work was done no set of differential varieties had been established for the identification of physiological races of *P. anomala*. In 1939 d'Oliveira published a list of eleven varieties which served to distinguish between the 30 races that had been isolated in Europe up till that time. Through the courtesy of Dr. d'Oliveira, who kindly supplied us with seed, we have been able to compare certain Australian cultures with those occurring elsewhere.

The work that was done earlier suggested that more than one race of *P. anomala* is present here. Waterhouse (1927) found *Hordeum murinum* (*Hordeum leporinum*) to be resistant. Later (1929) he listed this same species as susceptible, and the logical explanation is that two different physiological races were involved when these tests were made, although variation in the host plant could have caused a similar result. We have tested collections of this organism on the above grass and so far have been unable to detect any differences between them. *Hordeum leporinum* has proved immune in all tests.

When d'Oliveira's varieties were inoculated the following reactions were obtained with rust collections from Werribee, Victoria; Lawes, Queensland; Wingen and Muswellbrook, N.S.W. The figures represent the usual designations used in cereal leaf rust studies and are comparable with d'Oliveira's own descriptions (see Table 1).

In some of these varieties it was apparent that the seed was not pure for its reactions to these collections of rust. *H. vulgare speciale*, Aegyptische 4-zellige and Oderbrucker were outstanding in this regard. There was clear evidence of both resistant

DD

TABLE 1.

Variety.	S.U. Accession Number.	Rust Reaction.
Brustedt's Schladener	B 244	0, 1
Hordeum vulgare speciale	B 245	0, 1, 2, 4
Friedrichswerther Berg Wintergerste	B 246	4
Australische Recka	B 247	0, 1
Lichtls Lechtaler .. .. ⋅. ..	B 248	4
Samaria 4-zeilige	B 249	4
Hordeum vulgare pallidum	B 250	4
Aegyptische 4-zeilige sommergerste	B 251	0, 1, 2, 4
Quinn C.I. 1024	B 252	0, 1, 2
Bolivia C.I. 1257	B 253	0, 1
Oderbrucker C.I. 940	B 254	0, 1

and susceptible plants in the pots of these varieties. *H. vulgare speciale* and Aegyptische 4-zeilige had approximately the same number of resistant and susceptible plants and they are accordingly designated 0, 1, 2, 4. Oderbrucker, although it contained a mixture of types, was in the main susceptible. Seed of Oderbrucker C.I. 940 which we had on hand, however, was uniformly resistant to rust and consequently the reaction has been left as 0, 1, although the seed from Portugal did not give precisely this reaction. The four collections that were compared on this series of varieties were also studied on other varieties listed by d'Oliveira. The reactions were (see Table 2):

TABLE 2.

Variety.	S.U. Accession Number.	Rust Reaction.
Hordeum hexastichum eurylepis	B 255	4
,, ,, *recens*..	B 256	0, 1, 2
Ackermann's Bavaria	B 257	4
Featherston C.I. 1120	B 258	0, 1
Malting C.I. 1129	B 259	0, 1
Hanna C.I. 906	B 260	4
Juliaca C.I. 1114	B 261	0, 1

The above results, together with those given earlier, indicate that these collections of rust represent a physiological race unlike any of the 30 reported from Europe. In addition they have been found to differ from the races 1 and 2 given by Mains (1932) for U.S.A. In order to compare the race to which these collections belong, with races from overseas, we have tested all the barley varieties that have been added to the University accession lists since the time of Waterhouse's report in 1927. Unfortunately no field results are available, but the following classification will serve to indicate seedling reactions to our collections of leaf rust. Certain varieties listed above are given for comparison in Table 3.

Among the varieties listed as resistant there is a considerable amount of variation, but in all cases the reaction is one where much flecking results and no fully susceptible pustules are formed. Those varieties given as moderately resistant can show quite a considerable development of rust. On the same leaf, however, there may be intermingled flecks (;) and 2- reactions and in isolated cases a pustule will develop which is indistinguishable from a fully susceptible type. However, when one becomes familiar with the varieties and their rust reaction there is seldom any doubt about the group for any particular variety.

TABLE 3.

Resistant	S.U. Accession Number.	Moderately Resistant.	S.U. Accession Number.	Susceptible.	S.U. Accession Number.
Featherston	B 129	Abyssinian	B 158	Abyssinian	B 124
Oderbrucker C.I. 940	B 130	Tennessee Winter ..	B 161	Athos	B 125
Oderbrucker C.I. 957	B 131	Ben Beardless	B 162	Club Hybrid	B 126
Unnamed C.I. 1347 ..	B 132	017	B 173	Gulmalaya	B 127
Malting C.I. 1129	B 133	Kwan	B 174	Smooth Awn × Beard-	
Manchuria C.I. 2330 ..	B 134	Welder	B 175	less × Reka	B 128
Hooded Spring C.I. 716	B 135	Arequipa C.I. 1256 ..	B 188	Goldfoil	B 167
Horsford C.I. 507 ..	B 136	Callas C.I. 240	B 138	Hanna	B 168
Horsford C.I. 877 ..	B 137	Mecknos Moroc C.I. 1379	B 139	Bel. 2971	B 171
Success	B 146	Peruvian C.I. 935 ..	B 140	Peatland	B 176
Pearl	B 148	Quinn C.I. 1024 ..	B 141	Nigrinudum	B 178
Alberta Beardless ..	B 189	Bolivia C.I. 1257 ..	B 142	Compana	B 186
Glabron C.I. 4577 ..	B 195	Unnamed C.I. 2329 ..	B 143	Atlas × Vaughn ..	B 187
Colsess IV	B 212	Juliaca C.I. 1114 ..	B 144	Californian Mariout	
Colsess V	B 213	Deputy	B 145	C.I. 3615	B 190
Afghanistan	B 221	Argentine	B 149	Chevron C.I. 1111 ..	B 191
Schladener	B 242	O.A.C. 7	B 150	Charlottetown 80 ..	B 192
		Karru	B 151	Comfort C.I. 2488 ..	B 193
		Algerian	B 152	Golden Pheasant ..	B 196
		Beldi	B 153	Leiorrinchum	B 197
		Coast	B 154	Newal	B 198
		Portuguese	B 155	Regal	B 199
		Smooth Awn × Reka ..	B 156	Velvet	B 203
		Sulu C.I. 1022 ..	B 200	Vaughn	B 204
		Success	B 201	Wisconsin 38	B 205
		Trebi	B 202	Nigrinudum I	B 206
		Coast II	B 210	Nudideficiens	B 207
				Minn. 72–8	B 208
				Minn. 84–7	B 209
				Coast III	B 211
				Heitmann's Surprise ..	B 222
				Black Hulless	B 224
				Hanna	B 225
				Bolsheriki	B 227
				Barbless	B 230
				Male sterile	B 231
				Gymnospermum ..	B 233
				Engawnless	B 234
				Triple Bearded Mariout	B 235
				Trebi 4	B 237
				Egypt	B 238
				Austral	B 239
				Berg	B 240
				Samaria	B 243

INHERITANCE STUDIES.

Two of the varieties listed by Waterhouse (1927) have been mainly considered in this work. They are Minn. II 21.15 Smooth Awn × Manchuria and No. 22. Seedlings of No. 22 under glass-house conditions at Sydney are not as resistant to leaf rust as those of Minn. II 21.15. The reaction of the latter is almost always characterized by the sharpest flecks, that of No. 22 varies from place to place on the leaf from a fleck (;) to a 2– reaction. This range, for convenience, has been designated an X type. This difference in the resistant reaction to leaf rust suggested that the character might be controlled by a non-allelic series of genes, as has been found for different types of resistance to *P. graminis Tritici* in the Kenya varieties of *T. vulgare*. (Watson and Waterhouse, 1945.)

Both of the above barley varieties have been crossed with susceptible types and each has been found to possess a single major gene which differentiates its particular type of

resistance from susceptibility. Smooth Awn × Manchuria and No. 22 were accordingly crossed together reciprocally, and as no difference was shown, both this cross and its reciprocal are considered together. The grains resulting from crossing were divided, some were grown at the Cowra Experiment Farm and others at the University of Sydney. These latter were tested as seedlings for their reaction to leaf rust and the reaction of Minn. II 21.15 was dominant. Seedlings of a small F_2 population of 101 plants were tested for leaf rust reaction in 1944 and later were transplanted to the field, the remaining F_2 grain was grown at Hawkesbury Agricultural College. Of the 101 F_2 plants that were inoculated, two escaped infection, 76 gave flecks, 16 gave an X reaction and 7 were fully susceptible. No rust developed on the F_2 plants in the field at Richmond on account of the drought that prevailed in 1944.

Both batches, the classified material from the University and the unclassified from Richmond, were grown in duplicate pots and tested with rust as F_3 progenies in 1945. Only 65 of the 101 tested F_2 plants produced progenies and the behaviour of these was as in Table 4.

TABLE 4.

	F₂ Reaction.				F₃ Reaction.		
Breeding Result.				Type of Reaction.	;	X	4
Homozygous	..	..	..	;	13		
Segregating	..	..	..	;, X, 4	17		
Segregating	..	..	..	; and X	18		
Homozygous	..	..	..	X	1	3	
Segregating	..	..	..	X and 4	2	6	1
Segregating	..	..	..	; and 4	2		
Homozygous	..	..	..	4			2
Total	..	..	..	—	53	9	3

These figures, although not large, can be explained on the assumption that the two single factors possessed by these two varieties are not allelic and are inherited independently. On the basis of the reaction of the F_1 plants the resistance of Minn. II 21.15 is epistatic to that of No. 22. Of the 16 plants of the X type only 9 produced an F_3 progeny. If these plants carry the factor of No. 22 either in the heterozygous or homozygous condition, then one plant in three should be homozygous for the X reaction and two should segregate for the X reaction and complete susceptibility. The results observed with these nine progenies fit the expectancy well. According to this explanation the double recessive genotype which produced susceptible plants in F_2 should give homozygous susceptible plants in F_3. One progeny segregated for the X reaction and apparently this plant was wrongly classified in F_2.

On the suggestion of Dr. D. W. Robertson the single factor for resistance which is present in Minn. II 21.15 and which gives plants with sharp flecks, has been designated Pa_1. The one possessed by No. 22, which allows some rust to develop, is Pa_2. If these factors are independent and show the dominance relations given above, the expected phenotype in F_2 and its F_3 progeny would be as in Table 5.

The ratio of 76:16:7 which was obtained on 99 F_2 plants agrees reasonably well with the 12:3:1 which would be expected. Further data to support this explanation were obtained when rust reactions were observed on 170 additional F_3 progenies arising from plants which were grown at Richmond and were unclassified in the F_2 generation.

TABLE 5.

F_2 Genotype.	Expected F_2 Phenotype.	Reaction Type.	Expected F_3 Segregation.	Reaction Type.
$Pa_1 Pa_1 Pa_2 Pa_2$	Resistant.	;	Homozygous resistant.	;
$Pa_1 Pa_1 Pa_2 pa_2$	,,	;	Homozygous resistant.	;
$Pa_1 pa_1 Pa_2 Pa_2$ ..	,,	;	Segregating.	; and X
$Pa_1 pa_1 Pa_2 pa_2$	,,	;	Segregating.	;, X, 4
$Pa_1 Pa_1 pa_2 pa_2$	,,	;	Homozygous resistant.	;
$Pa_1 pa_1 pa_2 pa_2$	,,	;	Segregating.	; and 4
$pa_1 pa_1 Pa_2 Pa_2$	Moderately resistant.	X	Homozygous resistant	X
$pa_1 pa_1 Pa_2 pa_2$	Moderately resistant.	X	Segregating.	X and 4
$pa_1 pa_1 pa_2 pa_2$	Susceptible.	4	Homozygous susceptible.	4

When the two groups of 65 and 170 were pooled the classification resulted as shown in Table 6.

TABLE 6.

F_2 Reaction.	Reaction Type.	Expectancy in 16.	Observed.	Expected.
Homozygous resistant ..	;	4	57	58.7500
Segregating	; and X	2	39	29.3750
Segregating	; and 4	2	18	29.3750
Segregating all types ..	;, X, 4	4	55	58.7500
Homozygous	X	1	18	14.6875
Segregating	X and 4	2	35	29.3750
Homozygous susceptible ..	4	1	13	14.6875
Total		16	235	235·0000

When χ^2 is calculated the value of 9·868 is found to have a probability between 0·20 and 0·10. From these data then it appears that both varieties are resistant to leaf rust, one is highly resistant, the other moderately resistant, a single major factor is present in both parents but the factors are inherited independently in crosses between them. Their rust reaction and proposed genotype would be as follows:

Parent.	Rust Reaction.	
Smooth Awn × Manchuria	Resistant.	$Pa_1 Pa_1 pa_2 pa_2$
No. 22	Moderately resistant.	$pa_1 pa_1 Pa_2 Pa_2$

Association with Other Characters.

The linkage relations of these two genes are at present under investigation. A number of crosses have been made in this connection but the genes so far have been

found to be inherited independently of all those other characters so far studied. In the cross studied here, for example, Minn. II 21.15 has smooth awns, short rachilla hairs and is susceptible to race 3 of powdery mildew (*Erysiphe graminis Hordei*); No. 22 has rough awns, long rachilla hairs and is moderately resistant to powdery mildew. In order to determine whether there was any association between characters the awn indices of roughness of both the parents and F_2 plants were found by the method described by Hayes et al. (1923). The results confirmed the two factor difference for roughness of awn already reported by other workers. The breeding behaviour of F_3 lines for resistance and susceptibility to rust was compared with awn character as in the following table, where 243 F_2 plants classified for their awn index were tested as F_3 lines for rust reaction.

		F_2 Awn Character.		
		Rough.	Intermediate Rough.	Smooth.
F_3 rust reaction.	Resistant or segregating.	171	43	11
	Susceptible ..	14	4	0
Total		185	47	11

χ^2 for independence gave a P value 0·50–0·70 and the characters were considered to be independent.

Similar classifications were made for other characters and none of them revealed any association with leaf rust resistance. The following table summarizes the P values that were obtained (Table 7):

TABLE 7.

Characters.	Number of Plants.	χ^2.	P.
Roughness of awn and rust resistance	243	0·937	0·50–0·70
Rachilla hairs and rust resistance ..	243	0·044	0·70–0·80
Powdery mildew and rust resistance	237	3·201	0·50–0·70
Roughness of awn and rachilla hairs	263	18·680	<0·001

The association between roughness of awn and rachilla hair length was confirmed but as the result was based on less than 300 plants, no linkage values are given.

Crosses with Other Varieties.

The parents used in this study have been crossed with several other leaf rust resistant varieties to determine any relationship in the resistance to this disease. In the crosses used although the seed setting was good, grain mites lowered the viability of the crossed grain between the time of harvesting and sowing and hence the F_2 populations are small. In spite of the fact that they are too small for final conclusions to be drawn, they are reported here as an indication of the type of result obtained (Table 8).

TABLE 8.

Parents.	Number of Plants.	Classification.
Minn. II 21.15 × Virginia Hooded C.I. 2290	46	All resistant.
Minn. II 21.15 × H. distichon rimpaui typica	228	,, ,,
Minn. II 21.15 × Featherston	101	,, ,,
Minn. II 21.15 × Oderbrucker C.I. 940	460	,, ,,
Minn. II 21.15 × Hooded Spring C.I. 716	188	,, ,,
Minn. II 21.15 × Horsford C.I. 507	68	,, ,,
Virginia Hooded C.I. 2290 × Minn. II 21.15	166	,, ,,
Minn. 184 Manchuria × Minn. II 21.15	701	,, ,,
H. vulgare aethiops typica × Minn. II 21.15	47	,, ,,
Featherston × Minn. II 21.15	308	,, ,,
Oderbrucker C.I. 940 × Minn. II 21.15	486	,, ,,
Brachytic chlorina rust resistant × H. distichon rimpaui typica	424	,, ,,
H. distichon rimpaui typica × Brachytic chlorina rust resistant	118	,, ,,
H. vulgare aethiops typica C.I. 2208 × Virginia Hooded C.I. 2290	201	,, ,,

	Number of Plants.	R.	M. R.	S.
H. vulgare aethiops typica C.I. 2208 × No. 22	54	42	8	4
Virginia Hooded C.I. 2209 × No. 22	55	38	14	3
Featherston × No. 22	52	41	7	4
Oderbrucker C.I. 940 × No. 22	52	35	16	1
No. 22 × Virginia Hooded C.I. 2290	62	44	15	3
No. 22 × Featherston	56	43	11	2
No. 22 × Hooded Spring C.I. 716	60	46	10	4

R., resistant; M.R., moderately resistant; S., susceptible.

Certain of these crosses were made without knowing the genetic make-up of the parents for rust resistance. Despite this and despite the small populations that were tested, the results obtained to date indicate that there are probably not a great number of loci involved in conveying resistance to *P. anomala*. All the varieties that give a reaction like Minn. II 21.15 failed to give any segregation when crossed with it. No. 22, on the other hand, obviously had a different type of resistance and gave segregation in all cases where a cross was made with a variety showing the Minn. II 21.15 type of resistance. Observations are now being made on material in which No. 22 has been crossed with other varieties having a similar type of resistance.

SUMMARY.

Several collections of barley leaf rust have been shown to be similar, but unlike any of the 30 races described from Europe. Using one of these collections on F_1, F_2 and F_3 material of a cross II 21.15 (Smooth Awn × Manchuria) × No. 22, it was found that the two single factors possessed by these parents are not allelic and are inherited independently. The factor in II 21.15 (Smooth Awn × Manchuria) has been called Pa_1 and that in No. 22 Pa_2. When Smooth Awn × Manchuria was crossed with a number of varieties having a similar type of resistance, no segregation occurred. It appears from preliminary observation that there are not many loci involved in giving resistance to *P. anomala*.

ACKNOWLEDGEMENTS.

References.

D'OLIVEIRA B., 1939.—Studies on *Puccinia anomala* Rost. I. Physiologic Races on Cultivated Barleys. *Ann. Appl. Biol.*, 26 : 56-82.

HAYES, H. K., STAKMAN, E. C., GRIFFEE, F., and CHRISTENSEN, J. J., 1923.—Reaction of barley varieties to *Helminthosporium sativum*. Part I. Varietal Reaction. Part II. Inheritance Studies in a cross between Lion and Manchuria. *Minn. Agr. Exp. Stat. Tech. Bull.*, 21.

MAINS, E. B., and MARTINI, MARY L., 1932.—Susceptibility of Barley to Leaf Rust (*Puccinia anomala*) and to Powdery Mildew (*Erysiphe graminis hordei*). *Unit. Stat. Dept. Agric. Tech. Bull.*, 295.

WATERHOUSE, W. L., 1927.—Studies in the Inheritance of Resistance to Leaf Rust, *Puccinia anomala* Rost., in Crosses of Barley. I. *J. Roy. Soc. N.S.W.*, lxi : 218-247.

————, 1929.—Australian Rust Studies. PROC. LINN. SOC. N.S.W., liv : 615-680.

WATSON, I. A., and WATERHOUSE, W. L., 1945.—A Third Factor for Resistance to *Puccinia graminis Tritici. Nature*, 155, 205.

xvi

ABSTRACT OF PROCEEDINGS.

ORDINARY MONTHLY MEETING.
26th March, 1947. *See p. xv.*

ORDINARY MONTHLY MEETING.
30th April, 1947. *See p. xv.*

ORDINARY MONTHLY MEETING.
28th May, 1947.

Dr. G. D. Osborne, President, occupied the Chair.

Mr. R. Endean, Eastwood; Mr. L. A. S. Johnson, Cheltenham; Mrs. Pearl R. Messmer, Lindfield (who had been a member of the Society from 1932 to 1943), and Mr. M. R. O. Millett, B.A., Canberra, A.C.T., were elected Ordinary Members of the Society.

The Donations and Exchanges received since the previous Monthly Meeting (30th April, 1947), amounting to 9 Volumes, 119 Parts or Numbers, 2 Bulletins, 6 Reports and 4 Pamphlets, received from 25 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. Studies on the Economic Biology of the Sand Whiting (*Sillago ciliata*). By K. W. Cleland.

2. The Calcium Content of Legume Root Nodules. By H. L. Jensen, Macleay Bacteriologist to the Society.

3. Australian Buprestidae: Notes and Description of Four New Species. By C. Deuquet, B.Com.

4. Revision of Australian Lepidoptera. Oecophoridae. xiv. By A. Jefferis Turner, M.D., F.R.E.S.

NOTES AND EXHIBITS.

Dr. J. A. Dulhunty exhibited and commented upon a series of specimens to illustrate the evolution of coal.

Mr. C. Deuquet exhibited a freak specimen of the Scarabaeid *Anoplostethus opalinus* Brullé from Collie, south of Perth, Western Australia, in which the right half was reddish-brown and the left half opalescent green. Normally both sexes of this species may be either entirely opalescent green or reddish-brown.

ORDINARY MONTHLY MEETING.
25th June, 1947.

Dr. G. D. Osborne, President, occupied the Chair.

Miss Enid G. Fenton, Gordon; Miss Marie E. Phillips, M.Sc., Clifton Gardens; Miss Barbara V. Richards, B.Sc., Bondi Junction, and Mr. Robert E. Winkworth, Haberfield, were elected Ordinary Members of the Society.

The President announced that the Council had accepted the resignation of Dr. N. S. Noble as Secretary of the Society in consequence of his appointment as Editor of the new scientific journals to be published by the Council for Scientific and Industrial Research, the resignation to take effect from 31st July, 1947.

The Donations and Exchanges received since the previous Monthly Meeting (28th May, 1947), amounting to 3 Volumes, 28 Parts or Numbers, and 6 Bulletins, received from 27 Societies and Institutions, were laid upon the table.

SYMPOSIUM.

"THE PHYSIOLOGY OF PLANT DISEASE."

Summary of Contributions of Principal Speakers.

1. Professor N. A. Burges:

Soft rot diseases are associated primarily with parenchymatous tissue and are caused by fungi or bacteria capable of excreting enzymes which bring about disintegration of the tissues. In parenchyma tissue the cementing substances in the cell walls are mainly pectic in nature and the excreted enzymes bring about the degradation of the pectic material. The products of the decomposition include arabinose, galactose and galacturonic acid which can be utilized by the pathogen. Breakdown of the tissue, however, leads to rupture of the cells so that the normal contents of the parenchyma also become available to the pathogen. In addition to the enzymes, most soft rot organisms also excrete a thermostable toxin which kills the host cells.

2. Dr. N. H. White:

Vascular wilt is caused by certain pathogenic species of *Fusarium* and *Verticillium* fungi, and bacteria, which invade the water-conducting tissue of plants. These pathogens first invade the root tissue and then penetrate to the water-conducting elements, but they do not destroy the roots. Once in the vascular system they bring about a series of physiological changes in the plant which result in its death. Although various hypotheses were propounded to explain these changes (such as the utilization of nutrients and the plugging of the vascular tissue by the pathogen) it is now known that they result from the production of a toxin by the pathogen. The toxin passes up in the transpiration stream in the plant and increases the permeability of the cells, eventually destroying their plasma membranes. This effect is most marked in the leaf tissue and brings about the loss of normal powers of water retention by the leaf protoplasts which results in the collapse of the tissue. Browning of the vascular tissue remote from the location of the pathogen, which is so characteristic of vascular-wilt disease, occurs before wilt symptoms become apparent. These toxins are thermostable and may be produced by vascular wilt pathogens as well as a variety of other fungi when grown on artificial media. Filtrates from these cause pathological wilting in cut shoots of a variety of plants and they behave as antibiotic substances. In vascular wilt of tomato recent work has shown that the toxin responsible for pathological wilting (lycomarasmine) is a polypeptide ($C_9H_{15}O_7N_8$).

NOTES AND EXHIBITS.

Mr. E. Cheel exhibited herbarium specimens of "Tea-tree" (*Leptospermum floribundum* Salisb. 1796, and *L. juniperinum* Sm. 1797), which are united with *L. scoparium* by Bentham, *Fl. Aust.*, 1866. During a visit to New Zealand he collected specimens of the true *L. scoparium* Forst. (*Char. Gen.*, p. 72, Tab. 36, 1776), and several named varieties cultivated by nurserymen, which are quite distinct from the so-called *L. scoparium* recorded for Australia. Seedling plants raised from seeds from plants collected in National Park, near Sydney, and from Blackman's Bay, Tasmania, collected by Dr. H. D. Gordon, were also exhibited for comparison. *Leptospermum persiciflorum* Reichb. 1835, which is quite common on the north side of Sydney Harbour, is also included under *L. scoparium* by Bentham, and is illustrated in *Bot. Mag.*, at Tab. 3419, as *L. scoparium* var. *grandiflorum*. It has been cultivated at Ashfield and Hill Top, N.S.W. It flowers quite freely at Hill Top, but although it produced vigorous growth at Ashfield, the plant eventualy died. Specimens of *Melaleuca viridiflora* Gaertn., cultivated at Concord West, raised from seed collected at Evans Head, were also exhibited.

ORDINARY MONTHLY MEETING.

30th July, 1947.

Dr. G. D. Osborne, President, occupied the Chair.

Miss Peggy J. Bradhurst, B.Sc., Roseville; Mr. A. B. Costin, Roseville, and Mr. John T. Waterhouse, B.Sc., University of Sydney, were elected Ordinary Members of the Society.

The President, on behalf of members, offered congratulations to Miss June Lascelles, M.Sc., on her award of an 1851 Exhibition Scholarship.

The President referred to the death, on 18th July, 1947, of Mr. T. H. Pincombe, B.A., who had been a member of the Society since 1920.

The Donations and Exchanges received since the previous Monthly Meeting (25th June, 1947), amounting to 5 Volumes, 91 Parts or Numbers, 5 Bulletins and 2 Pamphlets, received from 36 Societies and Institutions and 1 private donor, were laid upon the table.

PAPERS READ.

1. Some Observations on the Cytology of Oogenesis in the Sydney Rock Oyster (*Ostrea commercialis* l. & R.). By K. W. Cleland.

2. On Fossil Leaves (Oleaceae) and a New Type of Fossil Pollen Grain from Australian Brown Coal Deposits. By Isabel C. Cookson, D.Sc. (*Communicated by Dr. W. R. Browne.*)

3. Fossil Fungi from Tertiary Deposits in the Southern Hemisphere. Part i. By Isabel C. Cookson, D.Sc. (*Communicated by Dr. W. R. Browne.*)

4. The Diptera of the Territory of New Guinea. xiv. Family Tabanidae. Part ii. Pangoniinae, except the Genus *Chrysops*. By H. Oldroyd, M.A., F.R.E.S. (*Communicated by Dr. G. A. M. Heydon.*)

5. Miscellaneous Notes on Australian Diptera. xiii. The Origin of the *Vena Spuria*. By G. H. Hardy.

6. Petrological Studies in the Ordovician of New South Wales. iv. The Northern Extension of the North-east Victorian Metamorphic Complex. By Germaine A. Joplin, B.Sc., Ph.D.

ORDINARY MONTHLY MEETING.

24th SEPTEMBER, 1947.*

Dr. G. D. Osborne, President, in the Chair.

The President introduced Dr. Dorothy Carroll, who had recently been appointed Secretary of the Society.

Dr. S. J. Paramonov, Canberra, A.C.T., and Mrs. Judith Windridge, B.Sc., Neutral Bay, were elected Ordinary Members of the Society.

The President announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1948, from qualified candidates. Applications should be lodged with the Secretary not later than Wednesday, 5th November, 1947.

The Donations and Exchanges received since the previous Monthly Meeting (30th July, 1947), amounting to 39 Volumes, 196 Parts or Numbers, 14 Bulletins, 7 Reports and 2 Pamphlets, received from 66 Societies and Institutions, were laid upon the table.

PAPERS READ.

1. On Australian Coleoptera. Part I. By J. W. T. Armstrong.

2. Larval Smarididae (Acarina) from Australia and New Zealand. By R. V. Southcott, M.B., B.S.

3. Studies in the Metabolism of Normal and Regenerative Tissue of the Earthworm. By B. R. A. O'Brien.

4. A Review of the Genus *Dendrobium* (Orchidaceae) in Australia. By the Rev. H. M. R. Rupp, B.A., and Trevor E. Hunt.

NOTES AND EXHIBITS.

The Rev. H. M. R. Rupp exhibited two orchids: *Pterostylis Mitchellii* Lindl., and *Sarcanthus Beckleri* (F. Muell.) Rupp, collected at Castle Hill and National Park respectively.

An account of the Perth Meeting of the Australian and New Zealand Association for the Advancement of Science was given by Dr. A. B. Walkom.

ORDINARY MONTHLY MEETING.
29th OCTOBER, 1947.

Dr. G. D. Osborne in the Chair.

Dr. Dorothy Carroll was elected an Ordinary Member of the Society.

The President announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1948, from qualified candidates. Applications should be lodged with the Secretary not later than Wednesday, 5th November, 1947.

The President announced the issue of a Proclamation under the provisions of the Wild Flowers and Native Plants Protection Act, 1927-1945, protecting certain wild flowers and native plants for a further period of three years from 1st July, 1947.

The President also announced that the Society had received an invitation for its members to become members of the American Polar Society.

The Donations and Exchanges received since the previous Monthly Meeting (24th September, 1947), amounting to 20 Volumes, 55 Parts or Numbers, 7 Bulletins and 1 Pamphlet, received from 42 Societies and Institutions and 1 private donor, were laid upon the table.

PAPERS READ.

1. A New Species of *Strongyluris* (Nematoda) from the Stomach of a Lizard, *Diporiphora australis*. By P. D. Harwood. (*Communicated by Dr. G. A. M. Heydon.*)

2. Resistance to Barley Leaf Rust (*Puccinia anomala* Rost.). By I. A. Watson and F. C. Butler.

3. Australasian Ceratopogonidae (Diptera, Nematocera). Part I. Relation to Disease, Biology, General Characters and Generic Classification of the Family, with a Note on the Genus *Ceratopogon*. By D. J. Lee, B.Sc.

4. Australasian Ceratopogonidae (Diptera, Nematocera). Part II. The *Leptoconops* Group of Genera. By D. J. Lee, B.Sc.

5. Australasian Ceratopogonidae (Diptera, Nematocera). Part III. The *Bezzia* Group of Genera. By D. J. Lee, B.Sc.

6. Australasian Ceratopogonidae (Diptera, Nematocera). Part IV. The *Stilobezzia* Group of Genera. By D. J. Lee, B.Sc.

7. Nitrogen Fixation in Leguminous Plants. VII. The Nitrogen-fixing Activity of Root Nodule Tissue in *Medicago* and *Trifolium*. By H. L. Jensen, Macleay Bacteriologist to the Society.

Dr. Ida Brown gave a talk, illustrated with numerous photographs, on "Some Palaeontological Research in the United States of America".

ORDINARY MONTHLY MEETING.
26th NOVEMBER, 1947.

Dr. G. D. Osborne, President, in the Chair.

The President announced that the Council had appointed Miss Muriel C. Morris, B.Sc. (Hons.), to a Linnean Macleay Fellowship in Zoology and Miss Mary D. Tindale, M.Sc., to a Linnean Macleay Fellowship in Botany for 1948.

The Donations and Exchanges received since the previous Monthly Meeting (29th October, 1947), amounting to 16 Volumes, 72 Parts or Numbers and 1 Bulletin, received from 32 Societies and Institutions and 1 private donor, were laid upon the table.

PAPERS READ.

1. The Influence of Molybdenum, Calcium and Agar on Nitrogen Fixation by *Azotobacter indicum*. By H. L. Jensen, formerly Macleay Bacteriologist to the Society.

2. Simuliidae (Diptera, Nematocera) from New Guinea, with the Description of One New Species. By R. H. Wharton, B.Sc.

Lecture: Mr. F. D. McCarthy gave a lecture on "Prehistoric Cultures of Australia", and exhibited a number of stone implements of various cultures to illustrate his lecture.

LIST OF MEMBERS.

(15th January, 1948.)

Ordinary Members.

1940 Abbie, Professor Andrew Arthur, M.D., B.S., B.Sc., Ph.D., c.o. University of Adelaide, Adelaide, South Australia.
1927 *Albert, Michel Francois, "Boomerang", 4½ Billyard Avenue, Elizabeth Bay, Sydney.
1940 *Allman, Stuart Leo, B.Sc.Agr., M.Sc., Entomological Branch. Department of Agriculture, Farrer Place, Sydney.
1922 Anderson, Robert Henry, B.Sc.Agr., Botanic Gardens, Sydney.
1899 Andrews, Ernest Clayton, B.A., F.R.S.N.Z., No. 4, "Kuring-gai", 241 Old South Head Road, Bondi, N.S.W.
1927 Armstrong, Jack Walter Trench, "Callubri", Nyngan, N.S.W.
1938 Ashby, Professor Eric, D.Sc., D.I.C., F.L.S., Botany Department, The University, Manchester, England.
1912 Aurousseau, Marcel, B.Sc., c.o. Mr. G. H. Aurousseau, 16 Woodland Street, Balgowlah, N.S.W.

1919 Barnett, Marcus Stanley, "The Hill", Victoria Street, Mount Victoria, N.S.W.
1935 *Beadle, Noel Charles William, D.Sc., Botany School, Sydney University.
1946 Bearup, Arthur Joseph, 66 Pacific Avenue, Penshurst, N.S.W.
1940 Beattie, Mrs. Joan Marion, M.Sc. (née Crockford), Bradley Street, Cobar, N.S.W.
1907 Benson, Professor William Noel, B.A., D.Sc., F.G.S., University of Otago, Dunedin, New Zealand.
1941 Blake, Stanley Thatcher, M.Sc., Botanic Gardens, Brisbane, Queensland.
1929 Boardman, William, M.Sc., Department of Zoology, University of Melbourne, Carlton, N.3, Victoria.
1946 Brett, Robert Gordon Lindsay, B.Sc., 7 Petty Street, West Hobart, Tasmania.
1923 Brough, Patrick, M.A., D.Sc., B.Sc.Agr., Botany School, Sydney University.
1924 Brown, Miss Ida Alison, D.Sc., Department of Geology, Sydney University.
1941 Browne, Miss Helen Rowan, 51 Nelson Street, Gordon, N.S.W.
1911 Browne, William Rowan, D.Sc., Department of Geology, Sydney University.
1947 Browning, T. O., Flat 31, "Selborne", 174 Phillip Street, Sydney.
1943 Bryan, Clement, B.A., Central School, Boorowa, N.S.W.
1931 *Burges, Professor Norman Alan, M.Sc., Ph.D., Botany School, Sydney University.
1945 Burgh, Henry Bertram, 4 Rose Crescent, Mosman, N.S.W.
1920 Burkitt, Professor Arthur Neville St. George Handcock, M.B., B.Sc., Medical School, Sydney University.

1927 Campbell, Thomas Graham, Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
1930 Carey, Miss Gladys, M.Sc., 32 Rawson Street, Epping, N.S.W.
1934 *Carey, Professor Samuel Warren, D.Sc., Geology Department, University of Tasmania, Hobart, Tasmania.
1905 Carne, Walter Mervyn, c.o. Department of Commerce and Agriculture, Reliance House, Flinders Lane, Melbourne, Victoria.
1947 Carroll, Miss Dorothy, B.A., B.Sc., Ph.D., D.I.C., Science House, 157 Gloucester Street, Sydney.
1936 *Chadwick, Clarence Earl, B.Sc., Entomological Branch, Department of Agriculture, Farrer Place, Sydney.
1899 Cheel, Edwin, 40 Queen Street, Ashfield, N.S.W.
1947 Christian, Stanley Hinton, c.o. Department of Public Health, Port Moresby, Papua-New Guinea.
1932 Churchward, John Gordon, B.Sc.Agr., Ph.D., 1 Hunter Street, Woolwich, N.S.W.
1946 Clark, Lawrance Ross, M.Sc., c.o. Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
1901 Cleland, Professor John Burton, M.D., Ch.M., University of Adelaide, Adelaide, South Australia.
1942 Cleland, Kenneth Wollaston, M.B., Department of Anatomy, Sydney University.
1931 Colefax, Allen Neville, B.Sc., Department of Zoology, Sydney University.
1946 Colless, Donald Henry, 45A Pacific Parade, Manly.
1942 Copland, Stephen John, B.Sc., 7 Creewood Street, North Strathfield, N.S.W.
1947 Costin, Alex Baillie, 12 Barambah Road, Roseville, N.S.W.
1908 Cotton, Professor Leo Arthur, M.A., D.Sc., Department of Geology, Sydney University.

* Life Member.

1928   Craft, Frank Alfred, B.Sc., 91 High Street, Taree, N.S.W.
1946   Crust, Miss Mabel, B.Sc., 21 Silex Road, Mosman, N.S.W.

1929   Dakin, Professor William John, D.Sc., Department of Zoology, Sydney University.
1945   Davis, Mrs. Gwenda Louise, B.Sc., 143 Mossman Street, Armidale, N.S.W.
1936   Day, Maxwell Frank, Ph.D., B.Sc., Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
1934   Day, William Eric, 23 Gelling Avenue, Strathfield, N.S.W.
1925   de Beuzeville, Wilfred Alexander Watt, J.P., "Melamere", Welham Street, Beecroft, N.S.W.
1937   Deuquet, Camille, B.Com., 126 Hurstville Road, Oatley, N.S.W.
1927   *Dixson, Sir William, "Merridong", 586 Gordon Road, Killara, N.S.W.
1937   Dulhunty, John Allan, D.Sc., Department of Geology, Sydney University.
1926   Dumigan, Edward Jarrett, State School, Toowoomba East, Queensland.
1946   Durie, Peter Harold, B.Sc., Regional Pastoral Laboratory, C.S.I.R. Mail Bag, Armidale, N.S.W.

1941   Edwards, Eric Thomas, Ph.D., M.Sc.Agr., National Press Pty. Ltd., 126-130 Phillip Street, Sydney.
1943   Ellison, Miss Dorothy Jean, M.Sc., Abbotsleigh College, Wahroonga, N.S.W.
1947   Endean, Robert, 15 Milton Avenue, Eastwood, N.S.W.
1930   English, Miss Kathleen Mary Isabel, B.Sc., 7 Dudley Road, Rose Bay, N.S.W.
1914   Enright, Walter John, B.A., P.O. Box 14, West Maitland, N.S.W.

1947   Fenton, Miss Enid Grace, 45 Cecil Street, Gordon, N.S.W.
1930   Fraser, Miss Lilian Ross, D.Sc., "Hopetoun", 25 Bellamy Street, Pennant Hills, N.S.W.

1935   *Garretty, Michael Duhan, M.Sc., 477 St. Kilda Road, Melbourne, S.C. 2, Victoria. Victoria.
1936   Gilmour, Darcy, M.Sc., 78 Boldrewood Street, Turner, A.C.T.
1944   Greenwood, William Frederick Neville, c.o. Colonial Sugar Refining Co. Ltd., Lautoka, Fiji.
1910   Griffiths, Edward L., B.Sc., 151 Wollongong Road, Arncliffe, N.S.W.
1936   Griffiths, Mervyn Edward, M.Sc., Australian Institute of Anatomy, Canberra, A.C.T.
1939   Gunther, Carl Ernest Mitchelmore, M.B., B.S., D.T.M., Bulolo, New Guinea.

1939   Hackney, Miss Frances Marie Veda, M.Sc., 40 Smith Street, Summer Hill, N.S.W.
1925   Hale, Herbert Matthew, South Australian Museum, Adelaide, South Australia.
1928   Hamilton, Edgar Alexander, 16 Hercules Street, Chatswood, N.S.W.
1917   Hardy, George Huddleston Hurlstone, "Waldheim", Waldheim Street, Annerley, Brisbane, S.3, Queensland.
1947   Harker, Miss Janet Elspeth, B.Sc., New England University College, Armidale, N.S.W.
1932   Harris, Miss Thistle Yolette, B.Sc., 14 Pacific Street, Watson's Bay, N.S.W.
1947   Henderson, David Leonard Wylie, L.S.M.I.S., "Craigstone", Woodford, N.S.W.
1930   Heydon, George Aloysius Makinson, M.B., Ch.M., Flat 5, 79 O'Sullivan Road, Rose Bay, N.S.W.
1938   Hill, Miss Dorothy, M.Sc., Ph.D., Department of Geology, University of Queensland, Brisbane, Queensland.
1943   Hindmarsh, Miss Mary Maclean, B.Sc., 78 Dover Road, Rose Bay, N.S.W.
1946   Holland, Victor Wallace, 39 Vaucluse Road, Vaucluse, N.S.W.
1930   Holmes, Professor James Macdonald, Ph.D., B.Sc., F.R.G.S., F.R.S.G.S., Department of Geography, Sydney University.
1943   Horowitz, Benzoln, Eng.Agr.S., Dr.Agr.Sc. (Cracow, Poland), Flat 24, No. 166 Victoria Road, Bellevue Hill, N.S.W.
1932   Hossfeld, Paul Samuel, M.Sc., 182 Fisher Street, Fullarton, South Australia.
1942   Humphrey, George Frederick, M.Sc., Molteno Institute, University of Cambridge, Cambridge, England.

1917   Jacobs, Ernest Godfried, "Cambria", 106 Bland Street, Ashfield, N.S.W.
1938   Jacobs, Maxwell Ralph, D.Ing., M.Sc., Dip.For., Commonwealth Forestry Bureau, Canberra, A.C.T.
1930   Jensen, Hans Laurits, D.Sc.Agr. (Copenhagen), State Laboratory of Plant Culture, Department of Bacteriology, Lyngby, Denmark.
1947   Johnson, Lawrence Alexander Sidney, 178 Beecroft Road, Cheltenham, N.S.W.
1945   Johnston, Arthur Nelson, B.Sc.Agr., Hawkesbury Agricultural College, Richmond, N.S.W.
1907   Johnston, Professor Thomas Harvey, M.A., D.Sc., F.L.S., University of Adelaide, Adelaide, South Australia.
1937   Jones, Mrs. Valerie Margaret Beresford, M.Sc. (née May), Botanic Gardens, Sydney.

* Life Member.

1930 Joplin, Miss Germaine Anne, B.Sc., Ph.D., "Huyton", 18 Wentworth Street, Eastwood, N.S.W.
1933 Judge, Leslie Arthur, No. 1 Bridge Road, Hornsby, N.S.W.

1937 Kesteven, Geoffrey Leighton, B.Sc., Fisheries Section, C.S.I.R., Marine Biological Laboratory, Cronulla, N.S.W.
1938 Kesteven, Hereward Leighton, D.Sc., M.D., The Hospital, Cooktown, Queensland.
1938 Kinghorn, James Roy, C.M.Z.S., Australian Museum, College Street, Sydney.

1939 Langford-Smith, Trevor, M.Sc., Ministry of Post-War Reconstruction, Canberra, A.C.T.
1946 Larcombe, Miss Pauline Gladys, B.Sc., 17 Ethel Street, Burwood, N.S.W.
1944 Lascelles, Miss June, M.Sc., 28 Jackson Street, Balgowlah, N.S.W.
1946 Lawrence, James Joscelyn, B.Sc., 91 Boundary Street, Clovelly, N.S.W.
1932 Lawson, Albert Augustus, 9 Wilmot Street, Sydney.
1936 Lee, David Joseph, B.Sc., c.o. Department of Zoology, Sydney University.
1934 Lee, Mrs. Alma Theodora, M.Sc. (née Melvaine), 16A Raglan Street, Mosman, N.S.W.
1945 Liddell, Miss Jean, Department of Biology, University of Adelaide, Adelaide, South Australia.
1943 Lothian, Thomas Robert Noel, Botanic Gardens, Adelaide, South Australia.

1945 Mackerras, David, 5 Edwards Bay Road, Mosman, N.S.W.
1922 Mackerras, Ian Murray, M.B., Ch.M., B.Sc., Veterinary Research Station, Yeerongpilly, Queensland.
1931 *Mair, Herbert Knowles Charles, B.Sc., 5 Collaroy Street, Collaroy Beach, N.S.W.
1939 Marshall, Alan John, Department of Zoology, University Museum, Oxford, England.
1932 Martin, Donald, B.Sc., Box 17, Huonville, Tasmania.
1905 Mawson, Sir Douglas, D.Sc., B.E., F.R.S., University of Adelaide, Adelaide, South Australia.
1933 Maze, Wilson Harold, M.Sc., Department of Geography, Sydney University.
1932 McCulloch, Robert Nicholson, B.Sc.Agr., B.Sc., Roseworthy Agricultural College, Roseworthy, South Australia.
1927 McKie, Rev. Ernest Norman, B.A., The Manse, Guyra, N.S.W.
1947 McMillan, Bruce, 171 Lawson Street, Newcastle, N.S.W.
1947 McRoberts, Miss Helen May, B.Sc., 16 Grosvenor Road, Lindfield, N.S.W.
1944 Mercer, Frank Verdun, B.Sc., St. John's College, Cambridge University, Cambridge, England.
1947 Messmer, Mrs. Pearl Ray, 64 Treatts Road, Lindfield, N.S.W.
1937 Middleton, Bertram Lindsay, B.A., M.D., Bridge House, Murrurundi, N.S.W.
1938 Miller, David, Ph.D., M.Sc., F.R.S.N.Z., F.R.E.S., Cawthron Institute, Nelson, New Zealand.
1947 Millett, Mervyn Richard Oke, B.A., Forestry and Timber Bureau, Canberra, A.C.T.
1946 Millington, Richard James, 65 Mann Street, Armidale, N.S.W.
1947 Morris, Miss Muriel Catherine, B.Sc., Women's College, Newtown, N.S.W.
1944 Moye, Daniel George, B.Sc., Dip.Ed., Warragamba Dam, via Wallacia, N.S.W.
1939 Moye, Mrs. Joan, B.Sc. (née Johnston), Warragamba Dam, via Wallacia, N.S.W.
1926 Mungomery, Reginald William, c.o. Bureau of Sugar Experiment Stations, Department of Agriculture and Stock, Brisbane, B.7, Queensland.
1920 Musgrave, Anthony, F.R.E.S., Australian Museum, College Street, Sydney.

1939 Naylor, George Francis King, M.A., M.Sc., Dip.Ed., University of Queensland, Brisbane, Queensland.
1925 Newman, Ivor Vickery, M.Sc., Ph.D., F.R.M.S., F.L.S., Department of Botany, Victoria University College, Wellington, New Zealand.
1922 Nicholson, Alexander John, D.Sc., F.R.E.S., Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
1935 *Noble, Norman Scott, D.Sc.Agr., M.Sc., D.I.C., Science House, Gloucester and Essex Streets, Sydney.
1920 Noble, Robert Jackson, B.Sc.Agr., Ph.D., 32A Middle Harbour Road, Lindfield, N.S.W.
1912 North, David Sutherland, 42 Chelmsford Avenue, Lindfield, N.S.W.

1942 O'Brien, Brian Robert Alexander, 18 Kennedy Road, Austinmer, N.S.W.
1927 Oke, Charles George, 34 Bourke Street, Melbourne, C.1, Victoria.
1927 Osborn, Professor Theodore George Bentley, D.Sc., F.L.S., Professor of Botany, University of Oxford, Oxford, England.
1921 Osborne, George Davenport, D.Sc., Ph.D., Department of Geology, Sydney University.

1947 Paramonov, Sergey Jacques, D.Sc., Division of Economic Entomology, C.S.I.R., Box 109, Canberra, A.C.T.
1940 Pasfield, Gordon, B.Sc.Agr., 20 Cooper Street, Strathfield, N.S.W.

* Life Member.

1922   Perkins, Frederick Athol, B.Sc.Agr., Biology Department, University of Queensland, Brisbane, Queensland.
1947   Phillips, Miss Marie Elizabeth, M.Sc., Department of Botany, Sydney University.
1937   Plomley, Kenneth Francis, 50 Domain Street, South Yarra, Melbourne, Victoria.
1935   Pope, Miss Elizabeth Carington, M.Sc., Australian Museum, College Street, Sydney.
1918   Priestley, Professor Henry, M.D., Ch.M., B.Sc., Medical School, Sydney University.
1938   Pryor, Lindsay Dixon, M.Sc., Dip.For., c.o. Department of the Interior, Canberra, A.C.T.

1929   Raggatt, Harold George, D.Sc., 485 Bourke Street, Melbourne, Victoria.   •
1947   Richards, Miss Barbara Vivian, B.Sc., 10 Small Street, Bondi Junction, N.S.W.
1946   Riek, Edgar Frederick, B.Sc., Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
1940   Robbins, Mrs. Elizabeth Marie, M.Sc. (née Basnett), 344 Railway Terrace, Guildford, N.S.W.
1936   Roberts, Noel Lee, 43 Hannah Street, Beecroft, N.S.W.
1932   Robertson, Rutherford Ness, B.Sc., Ph.D., Food Preservation Research Laboratory, C.S.I.R., Private Mail Bag, Homebush, N.S.W.
1945   Roper, Jack, M.I.H.S., 651 Williams Street, Broken Hill, N.S.W.
1945   Ross, Donald Ford, c.o. Ross Bros. Pty. Ltd., 545-547 Kent Street, Sydney.
1925   Roughley, Theodore Cleveland, B.Sc., F.R.Z.S., Chief Secretary's Department, Box 30A, G.P.O., Sydney.

1932   Salter, Keith Eric Wellesley, B.Sc., "Hawthorn", 48 Abbotsford Road, Homebush, N.S.W.
1919   *Scammell, George Vance, B.Sc., 7 David Street, Clifton Gardens, N.S.W.
1947   Scott, Miss Beryl, B.Sc., 314 Rowe Street, Eastwood, N.S.W.
1928   Selby, Miss Doris Adeline, M.Sc., M.B., 11 Locksley Street, Killara, N.S.W.
1930   Sherrard, Mrs. Kathleen Margaret, M.Sc., 43 Robertson Road, Centennial Park, Sydney.
1947   Shipp, Erik, 59 William Edward Street, Longueville, N.S.W.
1937   Simpson, Arthur Cecil.
1916   Smith, Miss Vera Irwin, B.Sc., F.L.S., "Loana", Mt. Morris Street, Woolwich, N.S.W.
1943   Smith-White, Spencer, B.Sc.Agr., 7 Merriwa Street, Gordon, N.S.W.
1945   Southcott, Ronald Vernon, M.B., B.S., 12 Avenue Road, Unley Park, Adelaide, South Australia.
1942   Spencer, Terence Edward, 16 Attunga Street, Woollahra, N.S.W.
1937   Spencer, Mrs. Dora Margaret, M.Sc. (née Cumpston), 16 Attunga Street, Woollahra, N.S.W.
1926   Stanley, George Arthur Vickers, B.Sc., c.o. Messrs. Robison, Maxwell and Allen, 19 Bligh Street, Sydney.
1898   Stead, David G., "Boongarre", 14 Pacific Street, Watson's Bay, N.S.W.
1935   Still, Jack Leslie, B.Sc., Ph.D., Department of Biochemistry, Sydney University.
1911   *Sulman, Miss Florence, "Burrangong", McMahon's Point, N.S.W.
1944   Sykes, Stephen Myles, B.Sc.Agr., 209 Johnston Street, Annandale, N.S.W.

1940   Taylor, Keith Lind, B.Sc.Agr., Forestry Commission, Division of Wood Technology, 96 Harrington Street, Sydney.
1944   Thorpe, Ellis William Ray, B.Sc., Department of Geography, Sydney University.
1943   Tindale, Miss Mary Douglas, M.Sc., 60 Spruson Street, Neutral Bay, N.S.W.
1946   Tipper, John Duncan, A.M.I.E.Aust., Box 2770, G.P.O., Sydney.
1921   *Troughton, Ellis Le Geyt, C.M.Z.S., F.R.Z.S., Australian Museum, College Street, Sydney.
1902   Turner, A. Jefferis, M.D., F.R.E.S., Dauphin Terrace, Brisbane, Queensland.
1904   Turner, Rowland E., F.Z.S., F.R.E.S., c.o. Standard Bank of South Africa, Adderley Street, Cape Town, South Africa.

1917   Veitch, Robert, B.Sc., F.R.E.S., Department of Agriculture and Stock, William Street, Brisbane, Queensland.
1930   Vickery, Miss Joyce Winifred, M.Sc., Botanic Gardens, Sydney.
1940   Vincent, James Matthew, B.Sc.Agr., Dip.Bact., Faculty of Agriculture, Sydney University.
1934   Voisey, Alan Heywood, D.Sc., New England University College, Armidale, N.S.W.

1909   Walkom, Arthur Bache, D.Sc., Australian Museum, College Street, Sydney.
1946   Wallace, Murray McCadam Hay, B.Sc., P.O. Box 127, Katanning, Western Australia.
1930   Ward, Melbourne, Pasadena Flats, Cross Street, Double Bay, Sydney.
1911   Wardlaw, Henry Sloane Halcro, D.Sc., F.A.C.I., Department of Physiology, Sydney University.
1936   Waterhouse, Douglas Frew, M.Sc., Council for Scientific and Industrial Research, Box 109, Canberra, A.C.T.
1947   Waterhouse, John Teast, B.Sc., Department of Botany, Sydney University.

* Life Member.

1928   Waterhouse, Lionel Lawry, B.E., "Rarotonga", 42 Archer Street, Chatswood, N.S.W.
1927   Waterhouse, Professor Walter Lawry, D.Sc.Agr., M.C., D.I.C., Faculty of Agriculture,
           Sydney University.
1941   Watson, Irvine Armstrong, Ph.D., B.Sc.Agr., Faculty of Agriculture, Sydney University.
1941   Wearne, Walter Loutit, "Telarah", 6 Collingwood Street, Drummoyne, N.S.W.
1946   Wharton, Ronald Harry, B.Sc., c.o. Department of Zoology, Sydney University.
1926   *Whitley, Gilbert Percy, Australian Museum, College Street, Sydney.
1946   Wilkins, Miss Marjorie Jessie, B.Sc., 33 Muston Street, Mosman, N.S.W.
1947   Windridge, Mrs. Judith, B.Sc., Department of Geology, Sydney University.
1947   Winkworth, Robert Ernest, 24 Crescent Street, Haberfield, N.S.W.
1934   Womersley, Herbert, F.R.E.S., A.L.S., South Australian Museum, Adelaide, South
           Australia.
1932   Woodhill, Anthony Reeve, B.Sc.Agr., Department of Zoology, Sydney University.

1936   Zeck, Emil Herman, 694 Victoria Road, Ryde, N.S.W.

HONORARY MEMBER.

1923   Hill, Professor James Peter, D.Sc., F.R.S.Z., F.Z.S., F.R.S., Royal College of Surgeons,
           Lincoln's Inn Fields, London, W.C. 2, England.

CORRESPONDING MEMBERS.

1902   Broom, Robert, M.D., D.Sc., F.R.S., Transvaal Museum, Pretoria, Transvaal, South Africa.
1942   Rupp, Rev. Herman Montague Rucker, B.A., 24 Kameruka Road, Northbridge, N.S.W.
1943   Waterhouse, Gustavus Athol, D.Sc., B.E., F.R.E.S., c.o. Mrs. Millett, Illoura Avenue,
           Wahroonga, N.S.W.

      * Life Member.

LIST OF GENERA AND SPECIES DESCRIBED AS NEW IN THIS VOLUME.
(1947.)
Genera.

Species.

LIST OF PLATES.

PROCEEDINGS, 1947.

i–vi.—Bryozoa from the Lower Carboniferous.

vii.—Nitrogen Fixation by *Clostridium butyricum*.

viii–x.—Fossil Leaves from Australian Brown Coal.

xi–xiv.—Fossil Fungi from Tertiary Deposits in the Southern Hemisphere.

xv.—Geological Sketch Map of the Albury-Jingellic District.

xvi–xx.—Oogenesis in the Sydney Rock Oyster.

xxi–xxii.—Australasian Ceratopogonidae.

xxiii.—Effect of Molybdenum, Vanadium, Calcium, and Agar on Nitrogen-fixation by *Azotobacter indicum*.

GENERAL INDEX.

(1947.)